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EVOLUTIONARY STABILITY AND DYNAMIC STABILITY IN A CLASS OF EVOLUTIONARY NORMAL FORM GAMES

by

Franz J. Weissing

Abstract:

A complete game theoretical and dynamical analysis is given for a class of evolutionary normal form games which are called 'RSP–games' since they include the well–known 'Rock–Scissors–Paper' game. RSP–games induce a rich selection dynamics, but they are simple enough to allow a global analysis of their evolutionary properties. They provide an ideal illustration for the incongruities in the evolutionary predictions of evolutionary game theory and dynamic selection theory.

Every RSP–game has a unique interior Nash equilibrium strategy which is an ESS if and only if and only if the average binary payoffs of the game are all positive and not too different from one another. Dynamic stability with respect to the continuous replicator dynamics may be characterized by the much weaker requirement that the equilibrium payoff of the game has to be positive. The qualitative difference between evolutionary stability and dynamic stability is illustrated by the fact that every ESS can be transformed into a non–ESS attractor by means of a transformation which leaves the dynamics essentially invariant.

In all evolutionary normal form games, evolutionary stability of a fixed point implies dynamic stability with respect to the continuous replicator dynamics. Due to 'overshooting effects', this is generally not true for the discrete replicator dynamics. In contrast to all game theoretical concepts (including the ESS concept), discrete dynamic stability is not invariant with respect to positive linear transformations of payoffs. In fact, every ESS of an RSP–game can both be stabilized and destabilized by a transformation of payoffs. Quite generally, however, evolutionary stability implies discrete dynamic stability if selection is 'weak enough'.

In the continuous–time case, the interior fixed point of an RSP–game is either a global attractor, or a global repellor, or a global center. In contrast, the discrete replicator dynamics admits a much richer dynamics including stable non–equilibrium behaviour. The occurrence of stable and unstable limit cycles is demonstrated both numerically and analytically.

Some selection experiments in chemostats reveal that competition between different asexual strains of the yeast *Saccharomyces cerevisiae* leads to the same cyclical best reply structure that is characteristic for RSP–games. Possibly, Rock–Scissors–Paper–games are also played in non–human biological populations.

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1. Introduction

There are two main approaches towards the phenotypic analysis of frequency dependent natural selection. First, there is the approach of *evolutionary game theory*, which was introduced in 1973 by John Maynard Smith and George R. Price. In this theory, the dynamical process of natural selection is not modeled explicitly. Instead, the selective forces acting within a population are represented by a fitness function, which is then analysed according to the concept of an evolutionarily stable strategy or ESS. Later on, the static approach of evolutionary game theory has been complemented by a *dynamic stability analysis* of the replicator equations. Introduced by Peter D. Taylor and Leo B. Jonker in 1978, these equations specify a class of dynamical systems, which provide a simple dynamic description of a selection process. Usually, the investigation of the replicator dynamics centers around a stability analysis of their stationary solutions.

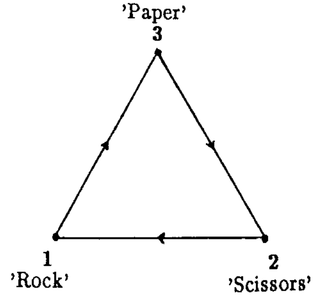
Although evolutionary stability and dynamic stability both intend to characterize the long–term outcome of frequency dependent selection, these concepts differ considerably in the 'philosophies' on which they are based. It is therefore not too surprising that they often lead to quite different evolutionary predictions (see, e.g., Weissing 1983). The present paper intends to illustrate the incongruities between the two approaches towards a phenotypic theory of natural selection. A detailed game theoretical and dynamical analysis is given for a generic class of evolutionary normal form games. In spite of its simplicity, this class is rich enough to uncover all kinds of discrepancies between evolutionary stability and dynamic stability. In the course of the analysis some light will be shed on the factors which are responsible for the inconsistencies in the conclusions of the game theoretical and the dynamical approach.

Evolutionary stability and dynamic stability correspond quite well to another if the number of pure strategies is small (Zeeman 1980, Weissing 1983). Discrepancies between these concepts may only be observed at a mixed Nash equilibrium strategy involving at least three pure strategies. Usually some form of cycling takes place around this equilibrium.[1] This suggests to have a closer look at the children's game *Rock–Scissors–Paper*, since this is the prototype example for a game where all these requirements are met.

In its simplest version, the Rock–Scissors–Paper game is modeled as a zero–sum game, which is represented by the payoff matrix

$$A = \begin{bmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{bmatrix}. \tag{1.1}$$

It is a characteristic property of this game that strategy i is always the unique best reply to strategy $i+1$ (counted modulo 3): Rock is optimal against Scissors, Scissors is optimal against Paper, and Paper is optimal against Rock. This cyclical pattern is symbolized in the following diagram:



(1.2)

In fact, (1.2) corresponds to the flow of the replicator dynamics on the border of the strategy simplex (see Figures 1 to 3), and it is plausible that a pattern like this implies the existence of an interior fixed point which is the center of a flow cycling around it.

However, if modeled as a zero–sum game, the Rock–Scissors–Paper game has some undesirable properties, which make it ill–suited as a 'counter–example'. It is easy to show that symmetric constant–sum games do not admit evolutionarily stable strategies. This corresponds well to the fact that interior fixed points of these games are always centers for the continuous and repellors for the discrete replicator dynamics (see Akin & Losert (1984), Hofbauer & Sigmund (1988), as well as Corollary 5.4 and Theorem 6.6 below).

We shall therefore leave the zero–sum context without abandoning the cyclical pattern described by diagram (1.2). Generalizing (1.1), we shall consider payoff matrices of the form

$$A = \begin{bmatrix} a_1 & b_2 & c_3 \\ c_1 & a_2 & b_3 \\ b_1 & c_2 & a_3 \end{bmatrix}, \quad b_i > a_i \geq c_i\,. \tag{1.3}$$

It will be shown that this is exactly the class of games to which diagram (1.2) does apply (see Theorem 3.4). A symmetric 3x3 normal form game which can be put into form (1.3) will be called a *generalized Rock–Scissors–Paper game* or simply an *RSP–game*. The evolutionary analysis of this class of games will form the subject–matter of this paper.[2]

More specific generalizations of the 'Rock–Scissors–Paper' game have repeatedly entered the literature. In particular, a one–parameter class of RSP–games plays a prominent role among the 'standard examples' of evolutionary game theory. It is the class of *ϵ–perturbed Rock–Scissors–Paper games*, which are characterized by payoff matrices of the form

$$A_\epsilon := \begin{bmatrix} 0 & 1+\epsilon & -1 \\ -1 & 0 & 1+\epsilon \\ 1+\epsilon & -1 & 0 \end{bmatrix}, \quad \epsilon > -1\,, \tag{1.4}$$

or by rescaled versions thereof.[3] Dating back to a paper of Maynard Smith (1977, quoting Dr. C. Strobeck), these games have been used to illustrate the fact that evolutionary stability need not imply dynamic stability with respect to the discrete replicator dynamics. In addition, they provide a nice illustration for the effects of a change in payoff parameters on the stability of an interior fixed point (see, e.g., Zeeman 1980).

An analysis of ϵ–perturbed Rock–Scissors–Paper games shows, however, that this class of 3x3–games is not rich enough for our purposes. In fact, the notions of evolutionary stability and 'continuous' dynamic stability coincide for these games (see Corollary 6.7). Since we are interested in getting *all* possible types of discrepancies between these concepts, we have to consider RSP–games in their most general form.

Certain aspects of the general class of RSP–games have previously been studied by Zeeman (1980), Weissing (1983), and Hofbauer & Sigmund (1988):

– Zeeman (1980) is mainly concerned with the classification of the phase portraits of evolutionary 3x3–games with respect to the continuous replicator dynamics. As a step towards this, he presents a global analysis of the phase portraits of RSP–games, and he shows that they may be classified according to the sign of a determinant. His results on RSP–games are contained in Section 5 below (Theorem 5.6). The proof given here, however, is constructive and has the advantage of focussing on the differences between evolutionary stability and dynamic stability.

– Complementing Zeeman's results on 'continuous stability', I investigated the conditions for evolutionary stability and discrete local hyperbolic stability (Weissing 1983). These aspects will be analysed in much more detail in Sections 4 and 6 below.

– In their excellent book on the replicator dynamics, Josef Hofbauer and Karl Sigmund (1988) give the most complete survey of stability properties of RSP–games. The results presented – which correspond to Theorems 3.4.2, 4.6.1, 5.6, and 6.8 below – extend to evolutionary stability as well as to dynamic stability with respect to both replicator dynamics. Since Hofbauer and Sigmund are focussing on more general dynamical aspects of natural selection, they do not prove their assertions, although the proofs are often far from being straightforward. Nevertheless, I owe much to their work. My own results and the analysis thereof have been improved considerably by adopting several of the techniques proposed in their book.

In the present paper, RSP–games will be put into a context that is more coherent and systematic than in the publications cited above. To my knowledge, it is the first time that a combined game theoretical and dynamical analysis is given for such a broad class of evolutionary normal form games.

The structure of this paper aims at exemplifying how the general methods developed in Hofbauer & Sigmund (1988) find natural applications in the analysis of concrete examples. By putting them into a broader context, the known features of RSP–games will be presented in a way that makes it easy to generalize them considerably.

In addition to providing new proofs for the known features of RSP–games, the present paper contains several results that do not have counterparts in the literature. In particular, almost all results on the discrete replicator dynamics (Sections 6, 7) seem to be new. For example, the occurence of supercritical Hopf bifurcations and 'closed limit curves' has not been observed before for the discrete replicator dynamics in two dimensions. Also the results on global discrete stability and instability have apparently not been derived before. In a separate paper (Weissing 1990) it will be shown that they apply quite generally to *all* evolutionary normal form games.

The main emphasis of the present paper will be put on elucidating the *qualitative differences* between evolutionary stability and dynamic stability, which are so well exemplified by the class of RSP–games. Among other things, the following results will be derived:

– With respect to the *continous* replicator dynamics, every ESS is a global attractor, but an asymptotically stable fixed point need not be an ESS. However, every asymptotically stable fixed point of an RSP–game – even if it is not an ESS – can be transformed into an ESS of another RSP–game by means of a transformation which leaves the phase portrait 'essentially' invariant. This shows that there is a qualitative difference between evolutionary stability and dynamic stability: the ESS concept is *not* invariant with respect to dynamics–preserving transformations of the state space (see Section 5.).

– With respect to the *discrete* replicator dynamics, evolutionary stability is neither necessary nor sufficient for dynamic stability. In fact, an ESS may be a global repellor, and a global attractor need not be an ESS. In the discrete context, we get an additional qualitative difference between evolutionary stability and dynamic stability: Whereas the ESS concept is invariant with respect to positive linear transformations of the payoff matrix, the stability properties with respect to the discrete replicator dynamics are very strongly affected by them. Indeed, any asymptotically stable fixed point of the discrete replicator equation can be destabilized by means of a positive linear transformation of payoffs (see Section 6).

– For the continuous replicator dynamics, *local* stability properties correspond perfectly to *global* stability properties. Generic Hopf bifurcations and limit cycles do not occur (Theorems 5.6 and 5.8). In the context of the discrete replicator dynamics, the same holds true for the subclass of 'circulant' RSP–games (Theorem 6.8). In general, however, supercritical Hopf bifurcations do occur, a fact which implies the existence of a more complicated attractor encircling the interior fixed point(see Section 7). Because of their simplicity, RSP–games provide one of the rare occasions where this phenomenon can be demonstrated analytically.

Taken together, these features show that RSP–games give an almost ideal illustration of the incongruities between the game theoretical and the dynamical approach towards frequency dependent natural selection. On the one hand, they are simple enough to allow an almost complete analysis of their evolutionary characteristics. In fact, there are no simpler games where all kinds of discrepancies between evolutionary stability and dynamic stability can be observed.[4] On the other hand, this class of games is rich enough to exemplify rather complex dynamical non–equilibrium behaviour like convergence to a closed limit curve.

2. Notation and Basic Definitions

We are interested in a situation where the fitness of individuals is affected by the outcome of a randomly assorted, binary, intra–specific interaction with the structure of an RSP–game. Each participant in an interaction behaves according to one out of three *pure strategies,* which will be called 'Rock', 'Scissors', and 'Paper' and numbered 1, 2, 3, respectively. Calculations with respect to this numbering should always be understood modulo 3. Pure strategies will always be denoted by the letters i and j, and the set of pure strategies will be denoted by I.

Mixed strategies (i.e., frequency distributions over the set of pure strategies) will be identified with the elements of the two–dimensional *strategy simplex*

$$\Delta := \{ \mathbf{p} \in \mathbb{R}^3_+ \mid \sum_i p_i = 1 \}. \tag{2.1}$$

Mixed strategies will be denoted by small bold–face letters like $\mathbf{p}$ or $\mathbf{q}$.

The set of pure strategies which is given a positive weight by the mixed strategy $\mathbf{p}$ is called the *support of* $\mathbf{p}$ and denoted by $\text{supp}(\mathbf{p})$:

$$\text{supp}(\mathbf{p}) := \{ i \in I \mid p_i > 0 \}. \tag{2.2}$$

As usual, the pure strategy $i \in I$ will be identified with the mixed strategy $\mathbf{e}^i \in \Delta$, the support of which consists of the single element i. Accordingly, the pure strategies correspond to the three 'corners' of the strategy simplex. A mixed strategy $\mathbf{p} \in \Delta$ will be called a *completeley mixed* or an *interior* strategy, if it has a 'full support', i.e., if $\text{supp}(\mathbf{p}) = I$.

The individuals interacting in an RSP–game form a population, the *state* of which is characterized by the frequency distribution of the pure strategies which are currently used by its members. Accordingly, a population state corresponds to a mixed strategy, the *population strategy.* A population, the state of which is given by population strategy $\mathbf{p} \in \Delta$, will be called a *p–population.*

A 3x3–matrix $A = (a_{ij})$ of the form (1.3) will be interpreted as the *payoff matrix* of an *evolutionary normal form game.* Since a symmetric bimatrix game is completely specified by the payoff matrix of player 1, we shall often identify an evolutionary game with this payoff matrix. The matrix entries are called the *binary payoffs* of the evolutionary game, and a_{ij} should be interpreted as the expected fitness of an individual using pure strategy i due to its interaction with an individual using pure strategy j.

Selection is *frequency dependent* whenever individual fitness is determined by the outcome of an evolutionary game. In fact, the fitness of an individual using pure strategy i depends on $\mathbf{p}$, the population strategy. Assuming that interacting individuals are assorted at random with respect to the strategies used, the individual fitness of an 'i–strategist' in a $\mathbf{p}$–population is given by

$$F_i(\mathbf{p}) := \sum_j a_{ij} p_j = (A\mathbf{p})_i \tag{2.3}$$

($(A\mathbf{p})_i$ denotes the i'th component of the vector $A\mathbf{p}$.). The vector

$$\mathbf{F}(\mathbf{p}) := A\mathbf{p} = \begin{bmatrix} a_1p_1 + b_2p_2 + c_3p_3 \\ c_1p_1 + a_2p_2 + b_3p_3 \\ b_1p_1 + c_2p_2 + a_3p_3 \end{bmatrix}, \tag{2.4}$$

the components of which are given by $F_i(\mathbf{p})$, is called the *fitness vector at* $\mathbf{p}$.

The fitness of an individual behaving according to mixed strategy $\mathbf{q}$ in a $\mathbf{p}$–population is given by

$$\mathcal{F}(\mathbf{q},\mathbf{p}) := \sum_i q_i F_i(\mathbf{p}) = \mathbf{q} \cdot \mathbf{F}(\mathbf{p}), \tag{2.5}$$

where the dot denotes the Euclidean scalar product. $\mathcal{F}(\mathbf{q},\mathbf{p})$ may also be interpreted as the mean fitness of a sub–population the strategy mix of which is described by $\mathbf{q}$. The function $\mathcal{F}\colon \Delta \times \Delta \longrightarrow \mathbb{R}$ which is defined by (2.5) is the *fitness function* of the evolutionary game. It corresponds to player 1's *payoff function* of the symmetric bimatrix game (A, A^T), where A^T denotes the transpose of the matrix A.

The *mean fitness* of a $\mathbf{p}$–population is given by

$$\overline{F}(\mathbf{p}) := \sum_i p_i \cdot F_i(\mathbf{p}) = \mathcal{F}(\mathbf{p},\mathbf{p}), \tag{2.6}$$

and the term $F_i(\mathbf{p}) - \overline{F}(\mathbf{p})$ will be interpreted as the *relative fitness* of strategy i in a $\mathbf{p}$–population.

The *replicator dynamics* intend to give a dynamic model of natural selection. There are two versions of it: a discrete one for the case of discrete and non–overlapping generations, and a continuous one for overlapping generations merging into another. Both versions are based on the assumption that the growth rate of a pure strategy is proportional to its relative fitness. A detailed derivation of the replicator dynamics and a discussion of the underlying assumptions may be found in Weissing (1983) and in Hofbauer and Sigmund (1988).

The continuous version of the replicator dynamics is given by a system of differential equations on the strategy simplex, which is called the *continuous replicator equation:*

$$\dot{p}_i := p_i \left(F_i(\mathbf{p}) - \overline{F}(\mathbf{p}) \right), \quad i \in I. \tag{2.7}$$

The discrete version of the replicator dynamics may be represented by a system of recursion equations, called the *discrete replicator equation:*

$$p_i' := p_i \frac{F_i(\mathbf{p})}{\overline{F}(\mathbf{p})}, \quad i \in I, \tag{2.8}$$

where $p' \in \Delta$ denotes the population strategy of an offspring population, the parents of which had $p \in \Delta$ as their population strategy.

The term *fitness* has a somewhat different interpretation in the two contexts: In the discrete case, the fitness of a character should be interpreted as the expected number of offspring of the individuals bearing this character. Correspondingly, only non–negative numbers make sense as fitness values. For the continuous replicator equation, there are no such restrictions on the fitness parameters, since the fitness of a character corresponds to its growth rate which may be positive or negative.

In what follows, we are interested in the fixed points of the replicator dynamics given by (2.7) and (2.8). A *fixed point* is a stationary solution of the replicator dynamics, i.e., a population strategy $p \in \Delta$, which satisfies the conditions

$$\dot{p}_i = 0 \quad (\text{or: } p_i' = p_i) \quad \text{for all } i \in I, \tag{2.9}$$

respectively. It is obvious that the discrete and the continuous version of the replicator dynamics have the same set of fixed points, and that a fixed point p^* of (2.7) or (2.8) is characterized by:

$$F_i(p^*) = \overline{F}(p^*) \quad \text{for } i \in \text{supp}(p^*)\,. \tag{2.10}$$

If p^* is a pure strategy, (2.10) always holds true. Pure strategies will be called the *trivial fixed points* of the replicator dynamics.

Notice that a completely mixed strategy p^* is an *interior fixed point* if and only if the fitness vector in p^* is a scalar multiple of the vector $1 := (1,1,\dots,1)$, i.e., if

$$F(p^*) = \lambda 1 \quad (\text{ where } \lambda = \overline{F}(p^*)\ ). \tag{2.11}$$

3. Nash Equilibrium Strategies of RSP–Games

In this section it will be shown that RSP–games may be characterized as those evolutionary 3x3 normal form games, for which the border of the strategy simplex does contain neither a Nash equilibrium strategy nor a nontrivial fixed point of the replicator dynamics. From this result it will be easy to derive that every RSP–game has a unique interior Nash equilibrium strategy. Subsequently, the coordinates of the interior fixed point will be characterized in terms of the entries of the payoff matrix.

DEFINITION 3.1: Nash equilibrium strategies.

A mixed strategy p^* is called a *Nash equilibrium strategy* or simply a *Nash strategy* if the strategy pair (p^*,p^*) is a symmetric Nash equilibrium point of the symmetric normal form game (A,A^T). Equivalently, p^* is a Nash strategy if it is a best reply to itself, i.e. if it satisfies the

Nash condition:
$$\mathcal{F}(p^*,p^*) \geq \mathcal{F}(q,p^*) \quad \text{for all } q \in \Delta. \tag{3.1}$$

For the interpretation of this concept, the reader is referred to van Damme (1987) or to Harsanyi & Selten (1988). The following proposition is a special case of the so–called Fundamental Lemma of non–cooperative game theory:

PROPOSITION 3.2: Characterization of Nash strategies.

p^* is a Nash equilibrium strategy if and only if the following conditions are satisfied:

$$F_i(p^*) = \overline{F}(p^*) \quad \text{for } i \in \text{supp}(p^*), \tag{3.2a}$$

$$F_i(p^*) \leq \overline{F}(p^*) \quad \text{for } i \notin \text{supp}(p^*). \tag{3.2b}$$

A comparison between (3.2) and (2.10) shows that every Nash strategy is a fixed point of the replicator dynamics. For a completely mixed strategy p^*, condition (3.2b) is empty. Accordingly, p^* is an *interior Nash strategy* if and only if it is an interior fixed point of the replicator dynamics, i.e., if and only if (2.11) holds true. On the other hand, fixed points of the replicator dynamics may be characterized as interior Nash strategies of substructures of A (see the proof of Theorem 3.4).

The following existence theorem is of fundamental importance. A proof of part 1. can be found in the classical paper of Nash (1951).

THEOREM 3.3: Existence of Nash equilibrium strategies.

1. For every evolutionary game there exists at least one Nash strategy.
2. If the border of the strategy simplex does not contain a Nash strategy, there exists a *unique* interior Nash strategy.

PROOF of Part 2.:

Since border Nash strategies do not exist, part 1. of the theorem implies the existence of at least one interior Nash strategy. Suppose that there are two interior Nash strategies, p_1^* and p_2^*.
By (2.11), this means that the fitness vectors $F(p_1^*)$ and $F(p_2^*)$ are scalar multiples of the vector 1. The linearity of F (see (2.3)) implies that $F(p)$ is also a scalar multiple of 1 for every strategy p of the form: $p = \mu_1 p_1^* + \mu_2 p_2^*$.

Correspondingly, all points of the intersection of the line L through p_1^* and p_2^* with the strategy simplex Δ are Nash equilibrium strategies as well. Since the intersection of L with the border of Δ is not empty, the border of Δ contains at least one Nash strategy.
This contradiction shows that the interior Nash strategy is unique.

* * *

THEOREM 3.4: Characterization of RSP–games.

1. A symmetric 3x3 normal form game is an RSP–game if and only if it has neither border Nash equilibrium strategies nor nontrivial border fixed points.
2. Every RSP–game has a unique interior Nash equilibrium strategy.[5]

PROOF:

A. By (3.2), a symmetric normal form game $A = (a_{ij})$ does not admit a pure Nash equilibrium strategy if and only if every column of A contains a on–diagonal element which is larger than the corresponding diagonal entry of A, i.e., if and only if the following holds true for every $i \in I$:

$$a_{ki} > a_{ii} \quad \text{for at least one } k \neq i. \tag{3.3}$$

B. A comparison of (2.10) and (3.2) shows that A does not admit a nontrivial border fixed point, if and only if none of its 2x2–restrictions has an interior Nash strategy. Here, a *2x2–restriction* of A is defined to be a 2x2 payoff matrix

$$A_{ij} = \begin{bmatrix} a_{ii} & a_{ij} \\ a_{ji} & a_{jj} \end{bmatrix}, \tag{3.4}$$

which results from A by removing one of its pure strategies from consideration.
It is easy to see that a symmetric 2x2 normal form game A_{ij} has an interior Nash strategy if and only if $(a_{ii}-a_{ji})$ and $(a_{jj}-a_{ij})$ have the same sign. Consequently, A_{ij} does not admit an interior Nash strategy if $(a_{ii}-a_{ji})$ and $(a_{jj}-a_{ij})$ differ in sign. Let us say that the pure strateg i *dominates* the pure strategy j if

$$a_{ii} \geq a_{ji} \quad \text{and} \quad a_{ij} \geq a_{jj}, \tag{3.5}$$

with at least one of these inequalities being strict. Accordingly, A_{ij} does not admit an interior Nash strategy if and only if one of its two pure strategies dominates the other.

C. It is clear from the definition of an RSP–game that none of its three pure strategies is a best reply to itself. Accordingly, RSP–games do not have pure Nash strategies.
On the other hand, all three 2x2–restrictions of an RSP–game have a dominating pure strategy. For example, 'Rock' dominates 'Scissors', if 'Paper' is removed from consideration. Therefore, RSP–games do not admit non–trivial border fixed points.

D. Let now $A = (a_{ij})$ denote a symmetric 3x3 normal form game which has no pure Nash strategies and no non–trivial border fixed points.
Since pure strategy 1 is not a Nash strategy, the first column of A contains an element which is larger than the diagonal entry a_{11}. Without loss in generality, we may assume $a_{31} > a_{11}$. (3.5) applied to the 2x2–restriction A_{13} yields $a_{33} \geq a_{13}$, since otherwise A_{13} would admit an interior Nash strategy.
In view of (3.3), the last inequality implies $a_{23} > a_{33}$, since otherwise strategy 3 would be a pure Nash strategy of A. Applying (3.5) to the 2x2–restriction A_{23}, we get $a_{22} \geq a_{32}$ which in turn implies $a_{12} > a_{22}$. Finally, we get $a_{11} \geq a_{21}$ by applying (3.5) to A_{12}. Summarizing all this, we have derived the following inequalities:

$$a_{31} > a_{11} \geq a_{21}, \quad a_{12} > a_{22} \geq a_{32}, \quad a_{23} > a_{33} \geq a_{13}. \tag{3.6}$$

which imply that A is the payoff matrix of an RSP–game.

E. Since RSP–games do not admit border Nash strategies, Theorem 3.3(2) shows that every RSP–game has a unique interior Nash strategy.[5]

* * *

In order to calculate the Nash strategies of a symmetric normal form game $A = (a_{ij})$, it is often useful to consider a rescaled version of that game. We shall perform a *positive linear transformation* of A, which is given by

$$\tilde{a}_{ij} := \lambda \cdot a_{ij} + \mu_j, \quad \mu = (\mu_1,\mu_2,\mu_3) \in \mathbb{R}^3, \ \lambda > 0. \tag{3.7}$$

A positive linear transformation is called *homogeneous*, if μ is a constant multiple of the vector $\mathbf{1}$. Two evolutionary games will be called *pl–equivalent* if one can be transformed into the other by means of a positive linear transformation.

PROPOSITION 3.5: Invariance with respect to positive linear transformations.

Pl–equivalent evolutionary normal form games have the same fixed points and the same Nash equilibrium strategies.

PROOF:

Let $\tilde{A} = (\tilde{a}_{ij})$ be defined by (3.7) and let $\tilde{\mathcal{F}}$ denote the fitness function induced by $\tilde{A}$. A simple calculation shows that $\tilde{\mathcal{F}}$ is related to $\mathcal{F}$ via

$$\tilde{\mathcal{F}}(\mathbf{q},\mathbf{p}) = \lambda\, \mathcal{F}(\mathbf{q},\mathbf{p}) + \mu \cdot \mathbf{p}, \quad \mathbf{q}, \mathbf{p} \in \Delta, \tag{3.8}$$

where the dot denotes the Euclidean scalar product. This implies

$$\tilde{\mathcal{F}}(q,p) - \tilde{\mathcal{F}}(p,p) = \lambda \cdot (\mathcal{F}(q,p) - \mathcal{F}(p,p)) . \tag{3.9}$$

Setting $q = e^i$, and denoting by $\tilde{F}$ and $\tilde{\bar{F}}$ the fitness vector and the mean fitness induced by $\tilde{A}$, we get

$$\tilde{F}_i(p) - \tilde{\bar{F}}(p) = \lambda \cdot (F_i(p) - \bar{F}(p)) . \tag{3.10}$$

In view of $\lambda > 0$, (2.10) and (3.2) show that A and $\tilde{A}$ have the same sets of fixed points and Nash equilibrium strategies. * * *

A slightly weaker version of this theorem is essential for 'classical' normative game theory: In normative game theory, payoffs are interpreted in terms of the utility concept of von Neumann and Morgenstern (see Luce & Raiffa 1957). This implies that payoffs are only well–defined up to homogeneous positive linear transformations. Consequently, it is a basic demand of normative game theory that all its solution concepts should be invariant with respect to this class of transformations.

Let us now focus again attention on the class of RSP–games. First, notice that the class of RSP–games is invariant under positive linear transformations of the payoff matrix. According to (1.3), every RSP–game is induced by a triple (a,b,c) of vectors which satisfy

$$a,b,c \in \mathbb{R}^3, \quad b_i > a_i \geq c_i \quad \text{for } i \in I . \tag{3.11}$$

A triple of vectors satisfying (3.11) will be called an *RSP–triple*. Whenever we want to emphasize the dependence of an RSP–game A on its generating RSP–triple (a,b,c) we shall write $A = A(a,b,c)$. Accordingly, $A(a,b,c)$ is given by

$$A(a,b,c) = \begin{bmatrix} a_1 & b_2 & c_3 \\ c_1 & a_2 & b_3 \\ b_1 & c_2 & a_3 \end{bmatrix} . \tag{3.12}$$

It will be useful to simplify a given RSP–game $A = A(a,b,c)$ by means of a positive linear transformation, which transforms the diagonal of A into zero. Setting $\lambda = 1$ and $\mu = -a$ in (3.7), we get a reprensentation of A in the form

$$A = A_0 + A_1 , \tag{3.13}$$

where A_0 is pl–equivalent to A and where A_1 denotes the matrix

$$A_1 = A(a,a,a) = \begin{bmatrix} a_1 & a_2 & a_3 \\ a_1 & a_2 & a_3 \\ a_1 & a_2 & a_3 \end{bmatrix} . \tag{3.14}$$

Since A_0 is pl–equivalent to A, it is also an RSP–game. It is given by

$$A_0 = A(0,\beta,-\gamma) = \begin{bmatrix} 0 & \beta_2 & -\gamma_3 \\ -\gamma_1 & 0 & \beta_3 \\ \beta_1 & -\gamma_2 & 0 \end{bmatrix}, \tag{3.15}$$

where β and γ denote non–negative vectors which are defined by

$$\beta_i := b_i - a_i > 0, \quad \gamma_i := a_i - c_i \geq 0, \quad i \in I. \tag{3.16}$$

For a given RSP–game, the decomposition (3.13) is unique. A_0 will be called the *interactive component* of A, whereas A_1 will be addressed as the *non–interactive component* of A. If A coincides with A_0, i.e., if its non–interactive component is zero, it will be called an *essential* RSP–game or an RSP–game in *essential form*.

It is obvious from the definition of mean fitness that it splits according to

$$\bar{F}(p) = \bar{F}_0(p) + \bar{F}_1(p), \quad p \in \Delta, \tag{3.17}$$

where $\bar{F}_0$ and $\bar{F}_1$ denote the mean fitness functions induced by A_0 and A_1. $\bar{F}_0(p)$ will be called the *interactive component* of mean fitness at p.

Let p^* denote the unique interior Nash strategy of A. Since A is pl–equivalent to A_0, p^* is also the unique interior Nash strategy of A_0. We shall now characterize p^* in terms of the entries of A_0, which are given by (3.16).

For the rest of this paper, the determinant of A_0 will play a crucial role. It is easy to see that it is given by

$$\det(A_0) = \beta_1\beta_2\beta_3 - \gamma_1\gamma_2\gamma_3. \tag{3.18}$$

(a) $\det(A_0) = 0$:

In order to characterize p^*, let us first consider the case $\det(A_0) = 0$. In view of (3.18), this is equivalent to $\gamma_1\gamma_2\gamma_3 = \beta_1\beta_2\beta_3 > 0$ which implies that the vector γ is strictly positive.
On the other hand, the kernel of A_0, $\ker(A_0)$, is nontrivial, i.e., there exists a real vector $y \in \mathbb{R}^3$, $y \neq 0$, such that $A_0 y = 0$. In coordinates, this is equivalent to

$$\beta_2 y_2 = \gamma_3 y_3, \quad \beta_3 y_3 = \gamma_1 y_1, \quad \beta_1 y_1 = \gamma_2 y_2. \tag{3.19}$$

In view of $\beta_i > 0$ and $\gamma_i > 0$, all components of vectors in $\ker(A_0)$ have the same sign. Accordingly, the linear space $\ker(A_0)$ corresponds to a straight line through 0 which completely belongs to $\mathbb{R}^3_+ \cup \mathbb{R}^3_-$, the union of the positive and the negative orthants of $\mathbb{R}^3$. Each such line has a unique intersection point with the strategy simplex. Let us denote the unique element of

$\Delta \cap \ker(A_0)$ by $\mathbf{p}^*$. Since $\mathbf{p}^*$ belongs to the kernel of A_0, the fitness vector at $\mathbf{p}^*$ coincides with the zero vector. In view of (2.11) and Theorem 3.4.2., this implies that $\mathbf{p}^*$ is the unique interior Nash equilibrium strategy of A_0.

We have shown that $\mathbf{p}^*$ is characterized by setting $\mathbf{p}^* = \mathbf{y}$ in (3.19) together with the condition that its components are positive and sum up to 1.

(b) $\det(A_0) \neq 0$:

Let us now assume that $\det(A_0) \neq 0$. This implies the existence of A_0^{-1}, the inverse of the matrix A_0. (2.3), (2.6) and (2.11) applied to A_0 and F_0 lead to

$$\mathbf{p}^* = \lambda\, A_0^{-1}\mathbf{1}, \text{ where } \lambda = \overline{F}_0(\mathbf{p}^*) = (\mathbf{1}\cdot A_0^{-1}\mathbf{1})^{-1} \tag{3.20}$$

A simple calculation shows that

$$A_0^{-1}\mathbf{1} = \frac{1}{\det(A_0)} \begin{bmatrix} \beta_2\beta_3 + \gamma_2\gamma_3 + \beta_3\gamma_2 \\ \beta_3\beta_1 + \gamma_3\gamma_1 + \beta_1\gamma_3 \\ \beta_1\beta_2 + \gamma_1\gamma_2 + \beta_2\gamma_1 \end{bmatrix}. \tag{3.21}$$

Note that for $\det(A_0) = 0$ as well as for $\det(A_0) \neq 0$ the following holds true:

$$\operatorname{sgn}[\overline{F}_0(\mathbf{p}^*)] = \operatorname{sgn}[\det(A_0)] = \operatorname{sgn}[\beta_1\beta_2\beta_3 - \gamma_1\gamma_2\gamma_3], \tag{3.22}$$

i.e., the determinant of A_0 has the same sign as the interactive component of the mean equilibrium payoff.

4. Evolutionary Stability in RSP–Games

In this section, we shall characterize the evolutionarily stable strategies of RSP–games. It will be shown that a Nash equilibrium strategy $\mathbf{p}^*$ is an ESS if and only if $\beta_{i+1} > \gamma_i$ holds true for all $i \in I$ and the terms $\beta_{i+1} - \gamma_i$ do not differ too much from one another in a sense to be made precise below. For $\mathbf{p}^*$ to be an ESS it is necessary but not sufficient that $\det(A_0)$, the determinant of the interactive component of the RSP–game A, is strictly positive.

DEFINITION 4.1: Evolutionarily stable strategies.

A mixed strategy $\mathbf{p}^* \in \Delta$ is an *evolutionarily stable strategy* or *ESS* if it satisfies the following two conditions:

1. *Nash condition :*

$$\mathcal{F}(\mathbf{p}^*,\mathbf{p}^*) \geq \mathcal{F}(\mathbf{q},\mathbf{p}^*) \quad \text{for all} \quad \mathbf{q} \in \Delta. \tag{4.1a}$$

2. ESS *condition :*

$$\mathcal{F}(\mathbf{p}^*,\mathbf{p}^*) = \mathcal{F}(\mathbf{q},\mathbf{p}^*) \text{ for } \mathbf{q} \neq \mathbf{p}^* \text{ implies } \mathcal{F}(\mathbf{p}^*,\mathbf{q}) > \mathcal{F}(\mathbf{q},\mathbf{q}). \tag{4.1b}$$

For the motivation of this concept see Maynard Smith (1982) or Weissing (1983). Since an ESS is a Nash equilibrium strategy satisfying the additional condition (4.1b), the ESS concept can formally be interpreted as a 'refinement' of the Nash equilibrium concept for symmetric normal form games (e.g., van Damme 1987).

A comparison of (4.1) with (3.9) shows that the concept of an evolutionarily stable strategy is invariant with respect to positive linear transformations of the payoff matrix. This implies that the unique interior Nash strategy of an RSP–game A is an ESS of A if and only if it is an ESS with respect to the interactive component A_0 of A.

The following theorem provides a characterization of evolutionarily stable strategies by means of a single 'local' condition, which plays an important role in the study of dynamic stability with respect to the continuous replicator dynamics. A proof of this theorem may be found in Hofbauer & Sigmund (1988) or in Weissing (1983).

THEOREM 4.2: Characterization of evolutionarily stable strategies.

1. $\mathbf{p}^*$ is an ESS if and only if there exists a neighbourhood $\mathbf{U}$ of $\mathbf{p}^*$ in Δ such that

$$\mathcal{F}(\mathbf{p}^*,\mathbf{q}) > \mathcal{F}(\mathbf{q},\mathbf{q}) \text{ for all } \mathbf{q} \in \mathbf{U},\ \mathbf{q} \neq \mathbf{p}^*. \tag{4.2}$$

2. An interior Nash equilibrium strategy is an ESS if and only if (4.2) holds true globally, i.e., if it holds true for $\mathbf{U} = \Delta$.

In Weissing (1990) it is shown that it is useful to introduce some notions of evolutionary instability. Specializing the definitions given there to the case of an *interior* Nash equilibrium strategy we get:

DEFINITION 4.3: Uniform evolutionary instability.

Let $\mathbf{p}^*$ denote an interior Nash strategy of the evolutionary normal form game A.

1. $\mathbf{p}^*$ is called *uniformly evolutionarily unstable* if the following holds true:

$$\mathcal{F}(\mathbf{p}^*,\mathbf{q}) \leq \mathcal{F}(\mathbf{q},\mathbf{q}) \text{ for all } \mathbf{q} \in \Delta. \tag{4.3}$$

2. $\mathbf{p}^*$ is called *definitely evolutionarily unstable* if

$$\mathcal{F}(\mathbf{p}^*,\mathbf{q}) < \mathcal{F}(\mathbf{q},\mathbf{q}) \text{ for all } \mathbf{q} \in \Delta,\ \mathbf{q} \neq \mathbf{p}^*. \tag{4.4}$$

3. $\mathbf{p}^*$ is called a *definite* Nash strategy, if it is either evolutionarily stable or definitely evolutionarily unstable.
4. $\mathbf{p}^*$ is called *neutral Nash strategy* if

$$\mathcal{F}(\mathbf{p}^*,\mathbf{q}) = \mathcal{F}(\mathbf{q},\mathbf{q}) \text{ for all } \mathbf{q} \in \Delta. \tag{4.5}$$

The terminology chosen is motivated by the next proposition where it is shown that the definiteness of an interior Nash strategy corresponds to the definiteness of the quadratic form which is induced by the payoff matrix A. In order to show this, let us interpret the population states $\mathbf{q} \neq \mathbf{p}^*$ as disturbances of the equilibrium state $\mathbf{p}^*$. Accordingly, they may be described as displacements of the form $\mathbf{q} = \mathbf{p}^* + \mathbf{x}$, where $\mathbf{x}$ is an element of the hyperplane

$$\mathbb{R}_0^n := \{ \mathbf{x} \in \mathbb{R}^n \mid \sum_i \mathbf{x}_i = 0 \}, \tag{4.6}$$

which may be interpreted as the 'tangent plane' to the strategy simplex Δ. Representing $\mathbf{q}$ in the form $\mathbf{q} = \mathbf{p}^* + \mathbf{x}$ and using the definition of the fitness function, we get:

$$\mathcal{F}(\mathbf{q},\mathbf{q}) - \mathcal{F}(\mathbf{p}^*,\mathbf{q}) = \mathbf{x} \cdot A\mathbf{p}^* + \mathbf{x} \cdot A\mathbf{x}. \tag{4.7}$$

For an interior fixed point, (2.11) yields

$$\mathbf{x} \cdot A\mathbf{p}^* = \lambda\, \mathbf{x} \cdot 1 = 0 \quad \text{for all } \mathbf{x} \in \mathbb{R}_0^n. \tag{4.8}$$

From Theorem 4.2 together with (4.7) and (4.8), we get the following result:

PROPOSITION 4.4: Characterization of interior ESS's.

Let $\mathbf{p}^*$ denote a completely mixed Nash equilibrium strategy of the evolutionary normal form game A. Then the following holds true:

1. $\mathbf{p}^*$ is an interior ESS if and only if the quadratic form induced by A is negative–definite when restricted to $\mathbb{R}_0^n$, i.e., if and only if

$$\mathbf{x} \cdot A\mathbf{x} < 0 \quad \text{for all } \mathbf{x} \in \mathbb{R}_0^n,\ \mathbf{x} \neq \mathbf{0}. \tag{4.9}$$

2. $\mathbf{p}^*$ is uniformly evolutionarily unstable if and only if this quadratic form is positive–semidefinite on $\mathbb{R}_0^n$. It is definitely evolutionarily unstable if and only if the form is positive–definite, and it is a neutral Nash strategy if and only if the form is identical to zero on this subspace.

There is a canonical isomorphism between $\mathbb{R}_0^n$ and $\mathbb{R}^{n-1}$ which may be characterized by the nx(n–1)–matrix

$$P = \begin{bmatrix} 1 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 1 \\ -1 & -1 & \cdots & -1 \end{bmatrix}, \quad p_{ij} := \begin{cases} \delta_{ij} & \text{for } i < n \\ -1 & \text{for } i = n \end{cases} \tag{4.10}$$

(δ_{ij} denotes the 'Kronecker delta'). With the help of P it is possible to transform the quadratic form $\mathbf{x} \cdot A\mathbf{x}$ on $\mathbb{R}_0^n$ to a quadratic form $\mathbf{y} \cdot A^*\mathbf{y}$ on $\mathbb{R}^{n-1}$. According to the transformation rules for quadratic forms, it is given by the (n–1)x(n–1)–matrix

$$A^* = P^T A\, P. \tag{4.11}$$

It is easy to see that the entries of $A^* = (a^*_{ij})$ are given by

$$a^*_{ij} := a_{ij} - a_{in} - a_{nj} + a_{nn}. \tag{4.12}$$

Let now A denote an RSP–game, the interactive component of which is given by A_0, and let $\mathbf{p}^*$ denote the unique interior Nash strategy of these games. Note that

$$P^T A\, P = P^T A_0\, P, \tag{4.13}$$

i.e., the quadratic forms on $\mathbb{R}^{n-1}$ induced by A and A_0 do not differ from another.

Theorem 4.4 shows that the definiteness of the Nash strategy $\mathbf{p}^*$ corresponds to the definiteness of the quadratic form induced by A^* on $\mathbb{R}^{n-1}$. It is well–known that the sign of this form can be derived from the sign of the eigenvalues of the symmetric matrix $S^* := A^* + (A^*)^T$: the quadratic form induced by A^* is positive (negative) definite if and only if all eigenvalues of S^* are positive (negative).

The sign of the eigenvalues of a symmetric 2x2–matrix can easily be derived from the signs of its trace and its determinant. Since the determinant of S^*, $\det(S^*)$, is equal to the product of its eigenvalues while its trace, $\mathrm{tr}(S^*)$, corresponds to their sum, we obtain the following result:

COROLLARY 4.5:

1. The interior fixed point $\mathbf{p}^*$ of an RSP–game is a definite Nash strategy if and only if $\det(S^*) > 0$.
2. $\mathbf{p}^*$ is an ESS if and only if $\det(S^*) > 0 > \mathrm{tr}(S^*)$.
3. $\mathbf{p}^*$ is definitely evolutionarily unstable if and only if $\det(S^*) > 0$ and $\mathrm{tr}(S^*) > 0$.
4. $\mathbf{p}^*$ is a neutral Nash strategy if and only if $\det(S^*) = \mathrm{tr}(S^*) = 0$.

A simple calculation shows that S^* is of the form

$$S^* = \begin{bmatrix} -2\delta_3 & \delta_1-\delta_2-\delta_3 \\ \delta_1-\delta_2-\delta_3 & -2\delta_2 \end{bmatrix}, \tag{4.14}$$

where the δ_i, i = 1,2,3, denote the terms

$$\delta_i := \beta_{i+1} - \gamma_i. \tag{4.15}$$

Trace and determinant of S^* are given by

$$\mathrm{tr}(S^*) = -2(\delta_2+\delta_3)\,, \tag{4.16}$$

$$\det(S^*) = 4\delta_2\delta_3-(\delta_1-\delta_2-\delta_3)^2. \tag{4.17}$$

Since we are free to rename pure strategies, there is no loss in generality if we assume

$$|\delta_1| \geq |\delta_2| \geq |\delta_3|\,. \tag{4.18}$$

In view of the inequality between the arithmetic and the geometric mean it is easy to derive the following implication from (4.17):

$$\det(S^*) > 0 \implies \mathrm{sgn}(\delta_1) = \mathrm{sgn}(\delta_2) = \mathrm{sgn}(\delta_3) \neq 0\,. \tag{4.19}$$

(3.18) together with (4.15) shows that $\det(A_0) > 0$, if all δ_i are positive. On the other hand, $\det(A_0) < 0$ holds true, if all the δ_i are negative. Therefore, (4.19) can be strengthened to

$$\det(S^*) > 0 \implies \mathrm{sgn}(\delta_i) = \mathrm{sgn}(\det(A_0)) \neq 0 \text{ for } i \in I\,. \tag{4.20}$$

If all δ_i have the same sign, the determinant of S^* may be written as

$$\det(S^*) = [(\sqrt{|\delta_2|}+\sqrt{|\delta_3|})^2-|\delta_1|]\cdot[|\delta_1|-(\sqrt{|\delta_2|}-\sqrt{|\delta_3|})^2]\,. \tag{4.21}$$

It is obvious from (4.18) that the second factor in (4.21) is positive. If all δ_i have the same sign, we therefore get

$$\mathrm{sgn}[\det(S^*)] = \mathrm{sgn}[\,(\sqrt{|\delta_2|}+\sqrt{|\delta_3|}) - \sqrt{|\delta_1|}\,]\,. \tag{4.22}$$

(4.22) motivates to introduce the term

$$\sigma(A_0) := \frac{\sqrt{|\delta_1|}}{(\sqrt{|\delta_2|}\;+\sqrt{|\delta_3|})}\,, \tag{4.23}$$

which will be called the *skewness* of the RSP–game A_0. In view of (4.18), the skewness of A may be interpreted as a measure for the variance between the three numbers $\sqrt{|\delta_1|}$, $\sqrt{|\delta_2|}$, and $\sqrt{|\delta_3|}$. Note that $\sigma(A_0)$ is smaller than one if and only if

$$(\sqrt{|\delta_2|}\;+\sqrt{|\delta_3|}) > \sqrt{|\delta_1|} \;\geq\; \sqrt{|\delta_2|} \;\geq\; \sqrt{|\delta_3|}, \tag{4.24}$$

i.e., if and only if the three numbers $\sqrt{|\delta_1|}$, $\sqrt{|\delta_2|}$, and $\sqrt{|\delta_3|}$ correspond to the lengths of the sides of a triangle. (Josef Hofbauer made me aware of this fact.)

The combination of (4.20), (4.22), and (4.23) yields

$$\det(S^*) > 0 \iff \sigma(A_0) < 1 \text{ and } \mathrm{sgn}(\delta_i) = \mathrm{sgn}(\det(A_0)) \neq 0. \tag{4.25}$$

On the other hand, $\det(S^*) = 0$ in combination with $\mathrm{tr}(S^*) = 0$ leads to

$$S^* = 0 \iff \mathrm{sgn}(\delta_i) = \mathrm{sgn}(\det(A_0)) = 0,\ i \in I. \tag{4.26}$$

In view of Corollary 4.5, (4.25) and (4.16) together with (4.26) yield the main result of this section:

Theorem 4.6: Evolutionary stability in RSP–games.

1. The unique interior Nash strategy $\mathbf{p}^*$ of an RSP–game A is an ESS if and only if

$$\sigma(A_0) < 1 \text{ and } \mathrm{sgn}[\beta_{i+1}-\gamma_i] = \mathrm{sgn}[\det(A_0)] > 0 \text{ for } i \in I. \tag{4.27}$$

2. $\mathbf{p}^*$ is definitely evolutionarily unstable if and only if

$$\sigma(A_0) < 1 \text{ and } \mathrm{sgn}[\beta_{i+1}-\gamma_i] = \mathrm{sgn}[\det(A_0)] < 0 \text{ for } i \in I. \tag{4.28}$$

3. $\mathbf{p}^*$ is a neutral Nash strategy if and only if

$$\mathrm{sgn}[\beta_{i+1}-\gamma_i] = \mathrm{sgn}[\det(A_0)] = 0 \text{ for } i \in I. \tag{4.29}$$

Note that $\beta_{i+1}-\gamma_i$ corresponds to the *sum* of the binary payoffs which the players get in the RSP–game A_0 whenever an i–strategist is paired with an $(i+1)$–strategist. Accordingly, $\mathbf{p}^*$ is an ESS if and only if the skewness of A is smaller than one and if the *mean* payoffs to the players in A_0 is always positive whenever different pure strategies meet one another. In view of (3.21), it is a necessary condition for $\mathbf{p}^*$ to be an ESS that the interactive component of mean fitness in $\mathbf{p}^*$ is positive. Notice also that (4.29) is equivalent to

$$A_0+A_0^{\mathrm{T}} = 0, \tag{4.30}$$

i.e., $\mathbf{p}^*$ is a neutral Nash strategy if and only if A_0 is a *zero–sum game.*

5. Stability with Respect to the Continuous Replicator Dynamics

In this section it will be shown that the stability behaviour of the interior fixed point $\mathbf{p}^*$ of an RSP–game A depends crucially on the sign of the determinant of its interactive component A_0: When $\det(A_0) > 0$, $\mathbf{p}^*$ is hyperbolically stable and even a global attractor. For $\det(A_0) = 0$, $\mathbf{p}^*$ is a global center, and the interior of the strategy simplex is filled with periodic orbits. When $\det(A_0) < 0$, $\mathbf{p}^*$ is hyperbolically unstable and a global repellor. This characterization will help to elucidate the discrepancies between evolutionary stability and 'continuous' dynamic stability since the sign of $\det(A_0)$ corresponds to the sign of the equilibrium payoff with respect to A_0.

In this section we deal with a continuous dynamical system, which is induced by an autonomous differential equation of the form

$$\dot{\mathbf{p}} = \mathbf{v}^A(\mathbf{p})\,. \tag{5.1}$$

$\mathbf{v}^A\colon \Delta \to \mathbb{R}^n_0$ denotes a vector field on Δ where for each given point $\mathbf{p} \in \Delta$ the space $\mathbb{R}^n_0$ should be interpreted as the tangent space to Δ at $\mathbf{p}$. The vector field is continuously differentiable and given by the continuous replicator dynamics, i.e., by

$$v_i^A(\mathbf{p}) := p_i\,(\,F_i(\mathbf{p}) - \overline{F}(\mathbf{p})\,),\quad i \in I\,. \tag{5.2}$$

A comparison of (5.2) with (3.10) shows that the continous replicator dynamics is essentially invariant with respect to positive linear transformations of the payoff matrix A. In fact, if the payoff matrices A and $\tilde{A}$ are related according to (3.7) we have

$$\mathbf{v}^{\tilde{A}}(\mathbf{p}) = \lambda\, \mathbf{v}^A(\mathbf{p}) \quad \text{for all } \mathbf{p} \in \Delta\,, \tag{5.3}$$

i.e., the tangent vectors given by the two vector fields are collinear for all $\mathbf{p}$. This implies that the dynamical systems induced by these two vector fields have the same phase portrait. The orbits of the two systems coincide – they are only passed with different velocities.

In particular, an RSP–game A is pl–equivalent to its interactive component A_0. In this case, we even have $\lambda = 1$, which implies that A and A_0 induce identical continuous replicator dynamics. Without loss in generality, we may therefore assume that A coincides with A_0, i.e., that it is an RSP–game in essential form.

In the rest of this section, we shall mainly be interested in the stability of fixed points: A fixed point $\mathbf{p}^*$ of a continuous dynamical system is called *(Lyapunov) stable* if orbits starting near $\mathbf{p}^*$ do not go too far away from $\mathbf{p}^*$. A fixed point $\mathbf{p}^*$ is called *attractive* if nearby starting orbits are attracted by $\mathbf{p}^*$. $\mathbf{p}^*$ is called *neutrally stable* if it is stable but not attractive, and it is called *asymptotically stable* if it is both stable and attractive. An interior fixed point $\mathbf{p}^*$ will be called a *global attractor* if it is stable and if it attracts *all* interior orbits. It will be called a *global repellor* if all interior non–equilibrium orbits converge to the boundary of the strategy simplex. Finally, it will be called a *global center* if it is neutrally stable and if the interior of the strategy simplex is filled with periodic orbits. Formal definitions of these concepts of dynamic stability can be found in every textbook on ordinary differential equations (e.g., Hirsch & Smale 1974).

A rather elegant technique for proving stability as well as instability of a fixed point $\mathbf{p}^*$ of a dynamical system is that of constructing a Lyapunov function for it. Formally, a *Lyapunov function* is a smooth scalar function V which has a strict local maximum in $\mathbf{p}^*$ and which has locally a *definite* sign along the orbits of the dynamical system. In order to make the last condition more precise, let $\{\mathbf{p}(t)\}$ denote an orbit of (5.1). At each point $\mathbf{p} = \mathbf{p}(t)$, the derivative of the map $t \mapsto V(\mathbf{p}(t))$ is given by

$$\dot{V}(\mathbf{p}) = \sum_i \frac{\partial V}{\partial x_i}(\mathbf{p})\; v_i^A(\mathbf{p}) = \operatorname{grad} V(\mathbf{p})\cdot \mathbf{v}^A(\mathbf{p}). \tag{5.4}$$

V increases near $\mathbf{p}^*$ along the orbits of (5.1), if and only if $\dot{V}(\mathbf{p}) > 0$ for all $\mathbf{p} \neq \mathbf{p}^*$ from a neighbourhood U of $\mathbf{p}^*$. If V has a strict local maximum in $\mathbf{p}^*$, the fixed point $\mathbf{p}^*$ is asymptotically stable in this case. $\mathbf{p}^*$ is unstable, if V decreases along nearby orbits, i.e., if $\dot{V}(\mathbf{p}) < 0$ for $\mathbf{p} \in U$, $\mathbf{p} \neq \mathbf{p}^*$. It is neutrally stable, if V is a *constant of motion* near $\mathbf{p}^*$, i.e., if $\dot{V}(\mathbf{p}) = 0$ for $\mathbf{p} \in U$. All these results and their implications for global stability may be found in many textbooks on dynamical systems (e.g., Bhatia & Szegö 1967).

Let $\mathbf{p}^*$ be an interior fixed point of (5.1). The scalar function $V\colon \Delta \longrightarrow \mathbb{R}$ defined on $\operatorname{int}(\Delta)$, the interior of Δ, by

$$V(\mathbf{q}) := \prod_i (q_i)^{p_i^*} \tag{5.5}$$

is a promising candidate for a Lyapunov function for the continuous replicator dynamics (5.1). In fact, it has a unique maximum in $\mathbf{p}^*$, and its time derivative at an interior strategy $\mathbf{q}$ is given by

$$\dot{V}(\mathbf{q}) = V(\mathbf{q})\,(\mathcal{F}(\mathbf{p}^*,\mathbf{q}) - \mathcal{F}(\mathbf{q},\mathbf{q})). \tag{5.6}$$

This shows that the function defined by (5.5) is a Lyapunov function for $\mathbf{p}^*$, whenever $\mathbf{p}^*$ is a definite Nash equilibrium strategy. Considering the remarks above, we get the following result, which is an obvious generalization of a theorem first proved by Hofbauer, Schuster & Sigmund (1979) and Zeeman (1980):

<u>THEOREM 5.1:</u> Evolutionary stability and dynamic stability.

For a definite or a neutral Nash equilibrium strategy $\mathbf{p}^*$ of an evolutionary normal form game A the notions of evolutionary stability and dynamic stability with respect to (5.1) coincide in the following sense:

1. If $\mathbf{p}^*$ is an ESS of A, it is an asymptotically stable fixed point of (5.1).
2. If $\mathbf{p}^*$ is definitely evolutionarily unstable, it is a repellor with respect to (5.1).
3. If $\mathbf{p}^*$ is a neutral Nash strategy, it is neutrally stable for (5.1).

For an interior definite Nash strategy, the local stability properties derived in Theorem 5.1 translate into global stability properties. In order to see this, let us write $\mathbf{q}$ in (5.6) in the form $\mathbf{q} = \mathbf{p}^* + \mathbf{x}$, where $\mathbf{x} \in \mathbb{R}^n_0$. Considering (4.7), (4.8), and (4.13), we get

$$\dot{V}(\mathbf{p}^* + \mathbf{x}) = -\,V(\mathbf{p}^* + \mathbf{x})\; \mathbf{x}\cdot A\mathbf{x} = -\,V(\mathbf{p}^* + \mathbf{x})\; \mathbf{x}\cdot A_0\mathbf{x}\,. \tag{5.7}$$

Proposition 4.4 shows that the scalar function V defined by (5.6) is a *global* Lyapunov function for $\mathbf{p}^*$, whenever $\mathbf{p}^*$ is a definite interior Nash strategy. This yields:

COROLLARY 5.2: Interior ESS's and global dynamic stability.

Let $\mathbf{p}^*$ denote an interior fixed point of the evolutionary normal form game A.

1. If $\mathbf{p}^*$ is an ESS of A, it is a global attractor of (5.1).
2. If $\mathbf{p}^*$ is definitely evolutionarily unstable, it is a global repellor for (5.1).
3. If $\mathbf{p}^*$ is a neutral Nash strategy, it is a global center for (5.1).

Let now A denote an RSP–game, let A_0 be its interactive component, and let δ_i, $i = 1,2,3$, be defined by (4.15), i.e., $\delta_i := \beta_{i+1}-\gamma_i$. Recall that the skewness of A_0, $\sigma(A_0)$, is given by (4.23). Let us set $\sigma(A_0) := 1/2$, if $\delta_1 = \delta_2 = \delta_3 = 0$. In view of Theorem 4.6, A will be called a *balanced RSP–game* if

$$\sigma(A_0) < 1 \quad \text{and} \quad \mathrm{sgn}[\beta_{i+1}-\gamma_i] = \mathrm{sgn}[\det(A_0)]. \text{ for all } i \in I. \tag{5.8}$$

Together with Theorem 4.6, Corollary 5.2 yields:

PROPOSITION 5.3: Stability in balanced RSP–games.

Let $\mathbf{p}^*$ denote the unique interior fixed point of the balanced RSP–game A. Then the following holds true:

1. $\mathbf{p}^*$ is an ESS if and only if $\det(A_0) > 0$. In this case, $\mathbf{p}^*$ is a global attractor with respect to the continuous replicator dynamics (5.1).
2. $\mathbf{p}^*$ is definitely evolutionarily unstable if and only if $\det(A_0) < 0$. In this case, it is a global repellor of (5.1).
3. $\mathbf{p}^*$ is a neutral Nash strategy if and only if $\det(A_0) = 0$. In this case, it is neutrally stable. In fact, it is a global center for (5.1).

It will be shown below that the dynamical features described in the preceding theorem are quite typical for RSP–games: the unique interior fixed point is either a global attractor, or a global repellor, or a global center with respect to the continuous replicator dynamics. The perfect correspondence between evolutionary stability and 'continuous' dynamic stability will be lost, however, as soon as we leave the class of balanced RSP–games.

In order to show this, we shall first consider a subclass of the class of balanced RSP–games. An RSP–game A will be called a *perfectly balanced RSP–game*, if the δ_i do not differ from one another, i.e., if

$$\delta_i = \beta_{i+1} - \gamma_i = \text{const} =: \delta. \tag{5.9}$$

Note that we have $\sigma(A_0) = 1/2 < 1$ for a perfectly balanced RSP–game and it is clear that the parameter δ has the same sign as $\det(A_0)$. This justifies the terminology chosen: every perfectly balanced RSP–game is a balanced game.

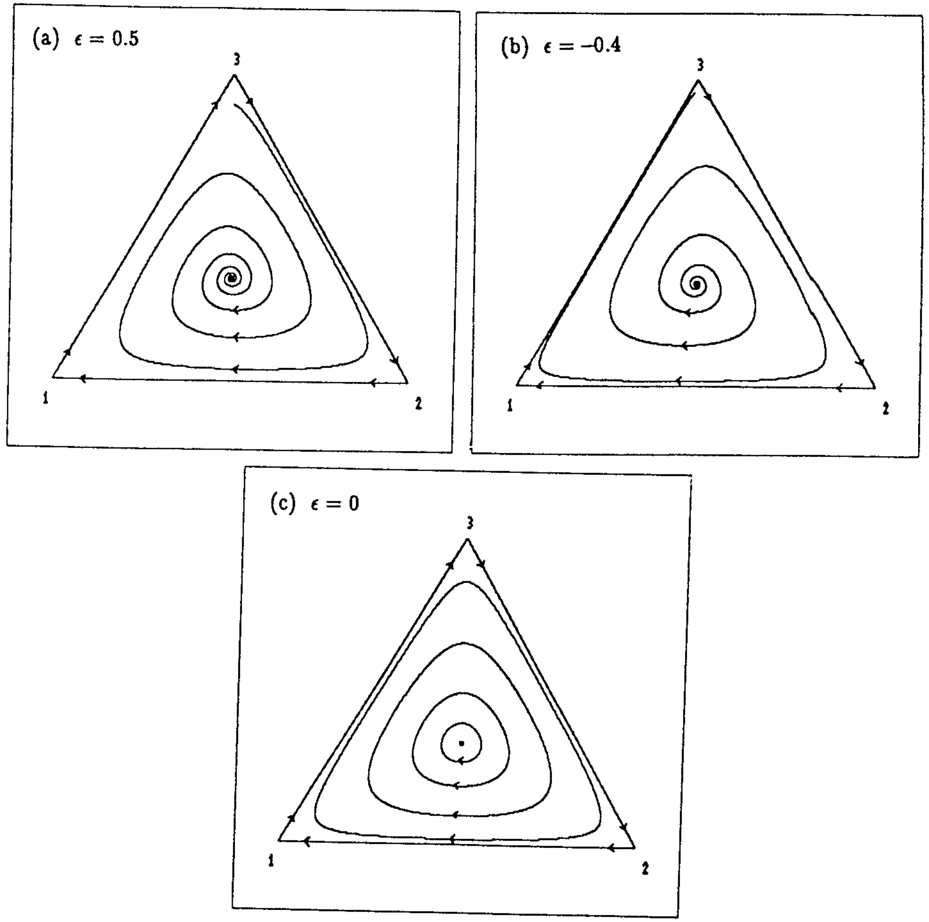


FIGURE 1: Continuous dynamic stability in ϵ–perturbed Rock–Scissors–Paper games.

(a) $\epsilon > 0$: $\mathbf{p}^*$ is an ESS and a global attractor.
(b) $\epsilon < 0$: $\mathbf{p}^*$ is definitely evolutionarily unstable and a global repellor.
(c) $\epsilon = 0$: $\mathbf{p}^*$ is a neutral Nash strategy and a global center.

The *ϵ-perturbed Rock-Scissors-Paper games* defined by (1.4) form a typical class of perfectly balanced RSP-games. In that case, δ corresponds to the parameter ϵ, and we have

$$\operatorname{sgn}[\det(A(\epsilon))] = \operatorname{sgn}(\epsilon)\ . \tag{5.10}$$

Accordingly, the interior fixed point of an ϵ-perturbed Rock-Scissors-Paper game is an ESS if and only if $\epsilon > 0$, and the notions of evolutionary stability and asymptotic stability with respect to (5.1) coincide (see Figure 1).

Constant-sum RSP-games form another class of perfectly balanced RSP-games. Slightly generalizing the concept as it is usually defined in game theory, a symmetric normal form game will be called a *constant-sum game* if

$$A_0 = -A_0^{\mathrm{T}}, \tag{5.11}$$

i.e., if its interactive component A_0 is a zero-sum game. From what has been shown above, we get:

COROLLARY 5.4: Stability in constant-sum RSP-games.

1. An RSP-game A is a constant-sum game if and only if it is a balanced RSP-game for which $\det(A_0) = 0$ holds true.
2. Constant-sum RSP-games do not admit an ESS. Their unique interior fixed point is always a global center with respect to (5.1).

In order to show that all RSP-games have similar stability properties with respect to the continuous replicator dynamics, we shall introduce a class of transformations by which every unbalanced RSP-game can be transformed into a balanced one: A *barycentric transformation* of the strategy simplex is a homeomorphism $\mathbf{x} \mapsto {}^{\pi}\mathbf{x}$ from Δ to itself, which is induced by a positive vector π and which is defined by

$${}^{\pi}x_i := \frac{x_i \pi_i}{\mathbf{x}\cdot\pi} \qquad (\pi_i > 0 \text{ for all } i \in I)\ . \tag{5.12}$$

It is easy to see that – up to a change in velocity – the transformation defined by (5.12) transforms the replicator dynamics (5.2) into another replicator dynamics which is induced by the payoff matrix (see Zeeman 1980)

$$A^{\pi} := A\cdot\operatorname{diag}(\pi^{-1}) \tag{5.13}$$

(π^{-1} denotes the vector $\pi^{-1} := (\pi_1^{-1},\dots,\pi_n^{-1})$, and $\operatorname{diag}(\mathbf{y})$ denotes a diagonal matrix, the diagonal of which is given by the vector $\mathbf{y}$).

The elements of $A^{\pi} = (a^{\pi}_{ij})$ are characterized by

$$a^{\pi}_{ij} = a_{ij}\pi_j^{-1}. \tag{5.14}$$

We say that A^{π} was derived from A *by means of a barycentric transformation.*

We have $\det(A^{\pi}) = \det(A)\cdot\det[\operatorname{diag}(\pi^{-1})]$. Therefore, the determinants of A and A^{π} are related via

$$\det(A^{\pi}) = \frac{1}{\pi_1\pi_2\pi_3}\det(A)\ . \tag{5.15}$$

Since π is a positive vector, it is clear that A^{π} is an RSP-game in essential form, if and only if A is an RSP-game in essential form.

THEOREM 5.5: Transformation into perfectly balanced games.

Every RSP-game $A = A_0$ in essential form can be transformed into a perfectly balanced RSP-game B_0 by means of a barycentric transformation. B_0 is also a game in essential form, and the determinants of the RSP-games A_0 and B_0 do not differ in sign:

$$\operatorname{sgn}[\det(B_0)] = \operatorname{sgn}[\det(A_0)]\ . \tag{5.16}$$

PROOF:
Let the RSP-game $A = A_0$ be of the form

$$A_0 = \begin{bmatrix} 0 & \beta_2 & -\gamma_3 \\ -\gamma_1 & 0 & \beta_3 \\ \beta_1 & -\gamma_2 & 0 \end{bmatrix}, \tag{5.17}$$

where $\beta_i > 0$, $\gamma_i \geq 0$ for $i = 1,2,3$. Let us also consider an auxiliary RSP-game in essential form, C_0, which is defined by

$$C_0 = \begin{bmatrix} 0 & \gamma_1 & -\beta_2 \\ -\beta_3 & 0 & \gamma_2 \\ \gamma_3 & -\beta_1 & 0 \end{bmatrix}. \tag{5.18}$$

Let $\mathbf{r}^*$ denote the unique interior fixed point of C_0. By (2.11) this means that $C_0\mathbf{r}^*$ is a scalar multiple of $\mathbf{1}$:

$$C_0\mathbf{r}^* = \lambda\,\mathbf{1}, \quad \text{where } \lambda = \mathbf{r}^*\cdot C_0\mathbf{r}^*. \tag{5.19}$$

After multiplication with (-1), the coordinate representation of (5.19) is given by

$$\begin{aligned} \beta_2 r_3^* - \gamma_1 r_2^* &= -\lambda, \\ \beta_3 r_1^* - \gamma_2 r_3^* &= -\lambda, \\ \beta_1 r_2^* - \gamma_3 r_1^* &= -\lambda. \end{aligned} \tag{5.20}$$

(5.20) motivates the following definition of B_0:

$$B_0 := \begin{bmatrix} 0 & \beta_2 r_3^* & -\gamma_3 r_1^* \\ -\gamma_1 r_2^* & 0 & \beta_3 r_1^* \\ \beta_1 r_2^* & -\gamma_2 r_3^* & 0 \end{bmatrix}. \tag{5.21}$$

We have $B_0 = A_0^{\pi}$, where the vector π is defined by

$$\pi_1 = (r_2^*)^{-1}; \ \pi_2 = (r_3^*)^{-1}; \ \pi_3 = (r_1^*)^{-1}. \tag{5.22}$$

(5.20) implies that B_0 is a perfectly balanced RSP–game: $\delta = -\lambda$, if $\delta = \delta(B_0)$ is defined by applying (4.15) to B_0. This shows that A_0 can be transformed into a perfectly balanced RSP–game by means of a barycentric transformation.

The only thing that remains to be shown is (5.16). This, however, follows directly from (5.15).

* * *

Let A_0 and B_0 be given as above. Since the phase portrait of $\mathbf{v}^{A_0}$ is the homeomorphic image of the phase portrait of $\mathbf{v}^{B_0}$, we get the following corollary from Theorem 5.3, which – due to its importance – will be stated as a theorem:

<u>Theorem 5.6:</u> 'Continuous' dynamic stability in RSP–games.

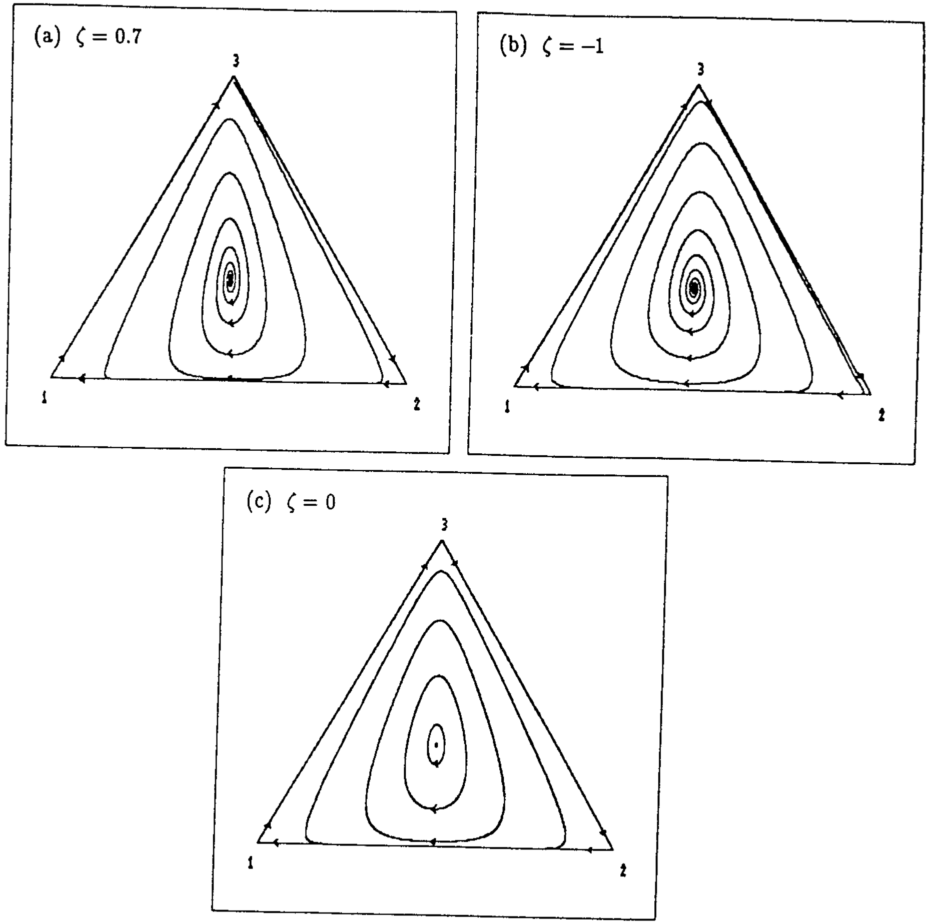
Let $\mathbf{p}^*$ denote the unique interior fixed point of the RSP–game A. Then the following holds true:

1. $\mathbf{p}^*$ is asymptotically stable for (5.1) if and only if $\det(A_0) > 0$. In this case, $\mathbf{p}^*$ is even a global attractor for the continuous replicator dynamics.
2. $\mathbf{p}^*$ is unstable for (5.1) if and only if $\det(A_0) < 0$. In this case, it is even a global repellor for the continuos replicator dynamics.
3. $\mathbf{p}^*$ is neutrally stable for (5.1) if and only if $\det(A_0) = 0$. In this case, it is a global center for the continuous replicator dynamics.

Theorem 5.6 is illustrated in Figure 2 by a one–parameter family of RSP–games which are given by payoff matrices of the form

$$A_0(\zeta) := \begin{bmatrix} 0 & 1 & \zeta-1 \\ \zeta-1 & 0 & 1 \\ 9 & \zeta-9 & 0 \end{bmatrix}, \quad \zeta \leq 1. \tag{5.23}$$

It is easy to see that all these games have the same interior fixed point $\mathbf{p}^* = (\frac{1}{3},\frac{1}{3},\frac{1}{3})$, and that the sign of $\det[A_0(\zeta)]$ is equal to the sign of ζ.



<u>Figure 2:</u> Continuous dynamic stability in the one–parameter family of RSP–games which are given by (5.23).

(a) $\zeta > 0$: $\mathbf{p}^*$ is a global attractor but not an ESS.
(b) $\zeta < 0$: $\mathbf{p}^*$ is a global repellor but not definitely evolutionarily unstable.
(c) $\zeta = 0$: $\mathbf{p}^*$ is a global center but not a neutral Nash strategy.

Note that for $\zeta > 0$, $\mathbf{p}^*$ is a global attractor for the continuous replicator dynamics, but it is not an ESS since $\delta_3 = \zeta - 8$ is a negative number (see Theorem 4.6). A comparison of Figures 1(a) and 2(a) gives an idea of why $\mathbf{p}^*$ is not an ESS: In Figure 2(a), the interior orbits approach the fixed point $\mathbf{p}^*$ on spirals with a high 'eccentricity'. All interior trajectories converge to $\mathbf{p}^*$, but they do so in a non–monotonical way. Near the 'minor axis' of the spiral, a trajectory comes very close to $\mathbf{p}^*$. Time and again, however, it departs from $\mathbf{p}^*$ on its way to the 'major axis' of the spiral. Such a behaviour is typical for attractors of the replicator dynamics which are *not* evolutionarily stable. In fact, evolutionarily stable strategies may be characterized as those stable fixed points of the continuous replicator dynamics which attract nearby orbits (locally) in a *monotonical* way.

A comparison of Theorems 4.6, 5.3, and 5.6 shows that it is just the class of balanced RSP–games, where the concepts of evolutionary stability and 'continuous' dynamic stability coincide. Whenever an RSP–game with $\det(A_0) > 0$ is balanced, the continuous replicator dynamics generates orbits with an 'eccentricity' which is small enough to ensure that the interior fixed point is approached in a monotonical way. If, however, one or more of the δ_i are negative, or if the skewness of A_0 is larger than one, the interior fixed point is not evolutionarily stable since there are always time periods where the trajectories temporarily depart from $\mathbf{p}^*$.

These observations have some important consequences: It is easy to construct an RSP–game which is not balanced but for which $\det(A_0) > 0$ holds true. For example, it is sufficient to choose δ_1, δ_2, and δ_3 all positive and in such a way that $\sigma(A)$, the skewness of A, is larger than one. For *any* such game, the unique interior fixed point $\mathbf{p}^*$ is a global attractor (Theorem 5.6), but it is not an ESS since (4.27) is not satisfied. According to Theorem 5.5, there exists a barycentric transformation which transforms $\mathbf{p}^*$ into the interior fixed point of a perfectly balanced RSP–game B. Since by (5.16) $\det(B) > 0$, the interior fixed point of B is an ESS (Theorem 5.3).

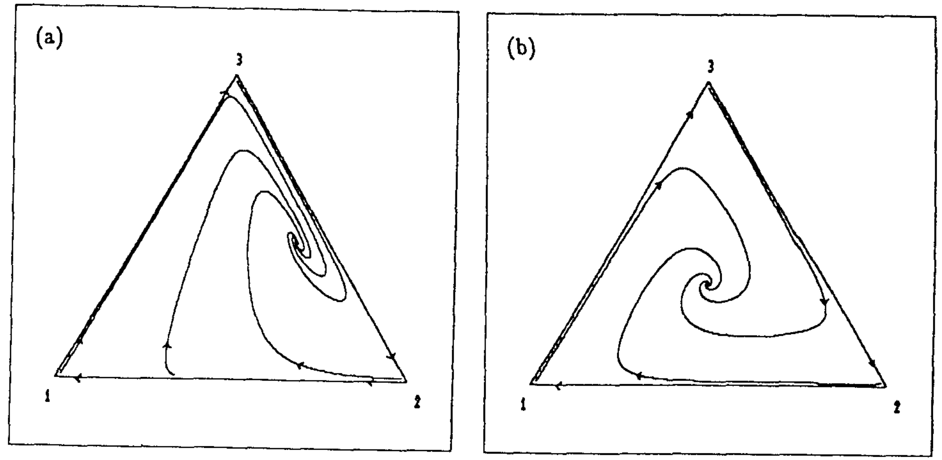
We have shown that there are Nash strategies which are not evolutionarily stable but which can nevertheless be transformed into an ESS (and vice versa) by means of a barycentric transformation of the state space – although barycentric transformations leave the dynamical features of the continuous replicator dynamics essentially invariant. This result, which is illustrated by Figure 3, will be stated as a Corollary:

<u>Corollary 5.7:</u> Evolutionary stability and barycentric transformations.

The concept of evolutionary stability is not invariant with respect to barycentric transformations of the strategy simplex.

We shall close this section by having a look at the linearization of (5.1) at the interior fixed point $\mathbf{p}^*$. Let

$$D := \mathrm{D}\mathbf{v}^A(\mathbf{p}^*) \tag{5.24}$$



<u>Figure 3:</u> Transformation of an evolutionarily unstable fixed point into an ESS by means of a barycentric transformation of the state space.

(a) Unbalanced RSP–game with payoff matrix and interior fixed point given by:

$$A = A_0 = \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 5 & 0 & 0 \end{bmatrix}, \quad \mathbf{p}^* = (\tfrac{1}{11}, \tfrac{5}{11}, \tfrac{5}{11}).$$

$\mathbf{p}^*$ is a global attractor, since $\det(A_0) = 5 > 0$.

$\mathbf{p}^*$ is not an ESS, since $\sigma(A_0) = \sqrt{5}/2 > 1$.

(b) Perfectly balanced RSP–game with payoff matrix and interior fixed point given by:

$$B = B_0 = \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \end{bmatrix}, \quad \mathbf{q}^* = (\tfrac{1}{3}, \tfrac{1}{3}, \tfrac{1}{3}).$$

$\mathbf{q}^*$ is a global attractor and an ESS of B.

Notice that B may be obtained from A by means of the barycentric transformation which is induced by the positive vector $\boldsymbol{\pi} = (5,1,1)$.

denote the derivative of the vector field $\mathbf{v}^A$ at $\mathbf{p}^*$. It is well–known that the stability behaviour of $\mathbf{p}^*$ with respect to (5.1) is closely related to the sign of the real parts of the eigenvalues of D (see, e.g., Hirsch & Smale 1974): A fixed point is asymptotically stable, if the real parts of all eigenvalues of D are negative, and it is unstable, if at least one of the eigenvalues of D has a positive real part. $\mathbf{p}^*$ is called a *hyperbolic fixed point*, if all the eigenvalues of D have a non–zero real part. A hyperbolic fixed point is stable if and only if all the eigenvalues of D are lying in the left half of the complex plane. In such a case, nearby orbits converge to $\mathbf{p}^*$ at an exponential rate, and the fixed point will be called *hyperbolically stable*. Slightly abusing terminology, $\mathbf{p}^*$ will be called *hyperbolically unstable*, if at least one eigenvalue of D has a positive real part.

If $\mathbb{R}^n_0$ is identified with $\mathbb{R}^{n-1}$ by means of the canonical isomorphism P described in (4.10), the linear map D can be characterized by its *Jacobian matrix* with respect to the canonical coordinates of $\mathbb{R}^{n-1}$. It should cause no confusion, if this matrix is also denoted by the letter D. It is shown in Weissing (1983) that the (n–1)x(n–1) Jacobian matrix $D = (d_{ij})$ of the vector field (5.2) at an interior fixed point is given by

$$d_{ij} := p^*_i \left(a^*_{ij} - \sum_k p^*_k \, a^*_{kj} \right), \tag{5.25}$$

where the summation extends over $k \in I$, $k < n$. $A^* = (a^*_{ij})$ denotes the (n–1)x(n–1) matrix given by (4.11). Note that in view of (4.13) it does not matter whether we consider the linearisation with respect to A or with respect to A_0.

It is obvious from (5.25) that the Jacobian D takes an especially simple form, if $\mathbf{p}^*$ coincides with the *barycenter* $\mathbf{m}$ of the strategy simplex, which is defined by

$$\mathbf{m} := \tfrac{1}{3}\cdot\mathbf{1} = (\tfrac{1}{3},\tfrac{1}{3},\tfrac{1}{3}). \tag{5.26}$$

Following Zeeman (1980), an RSP–game will be called a *central game*, if its unique interior fixed point coincides with the barycenter $\mathbf{m}$. In view of (2.11), an RSP–game A is a central game if and only if its row sums are equal to one another. The interactive component A_0 of a central RSP–game A is also a central game. More precisely: A is a central game if and only if

$$\eta_i = \beta_i - \gamma_{i+1} = \text{const} =: \eta, \quad \text{for } i \in I. \tag{5.27}$$

A simple calculation under consideration of (5.25) and (4.13) shows that for a central RSP–game the Jacobian D at the interior fixed point $\mathbf{p}^* = \mathbf{m}$ is of the form

$$D = \tfrac{1}{9}\begin{bmatrix} -\beta_1 + \beta_3 + \gamma_1 + 2\gamma_3 & 2\beta_2 + \beta_3 + \gamma_2 + 2\gamma_3 \\ -\beta_1 - 2\beta_3 - 2\gamma_1 - \gamma_3 & -\beta_2 - 2\beta_3 + \gamma_2 - \gamma_3 \end{bmatrix}. \tag{5.28}$$

Using (5.27), it is easy to see that the trace and the determinant of D are given by

$$\mathrm{tr}(D) = -\tfrac{1}{3}\,\eta, \tag{5.29}$$

$$\det(D) = \tfrac{1}{9}\left(\eta^2 + \boldsymbol{\beta}\cdot\boldsymbol{\gamma}\right). \tag{5.30}$$

It is well–known that the trace of a matrix corresponds to the sum of its eigenvalues while the determinant is identical to their product. Note that (5.29) and (5.30) imply

$$\det(D) > [\mathrm{tr}(D)]^2. \tag{5.31}$$

From this, we get immediately that the eigenvalues of D are complex conjugate to another. Correspondingly, their real parts have the same sign as $\mathrm{tr}(D)$. In view of (5.29), the interior fixed point $\mathbf{m}$ is hyperbolically stable if $\eta > 0$, and it is hyperbolically unstable if $\eta < 0$.

For any vector $\mathbf{y} \in \mathbb{R}^3$ let $\bar{\mathbf{y}} \in \mathbb{R}$ denote *the arithmetic mean of* $\mathbf{y}$, i.e.,

$$\bar{\mathbf{y}} := \tfrac{1}{3}\sum_i y_i = \mathbf{m}\cdot\mathbf{y}. \tag{5.32}$$

If $A = A(\mathbf{a},\mathbf{b},\mathbf{c})$ is a central RSP–game, and if $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ are given by (3.16), we get from (5.27):

$$\eta = \bar{\eta} = \bar{\beta} - \bar{\gamma} = \bar{\mathbf{b}} + \bar{\mathbf{c}} - 2\bar{\mathbf{a}}. \tag{5.33}$$

Combining this with the previous arguments, we have shown that:

<u>Proposition 5.8:</u> Hyperbolic stability in central RSP–games.

Let $A = A(\mathbf{a},\mathbf{b},\mathbf{c})$ be a central RSP–game. Then the following holds true:

1. The interior fixed point $\mathbf{p}^* = \mathbf{m}$ of A is hyperbolically stable with respect to the continuous replicator dynamics if and only if the arithmetic mean of the vectors $\mathbf{b}$ and $\mathbf{c}$ is larger than the arithmetic mean of the vector $\mathbf{a}$, i.e., if

$$\tfrac{1}{2}\cdot(\bar{\mathbf{b}} + \bar{\mathbf{c}}) > \bar{\mathbf{a}}. \tag{5.34}$$

2. $\mathbf{p}^*$ is hyperbolically unstable if and only if $\bar{\mathbf{a}}$ is larger than the mean of $\bar{\mathbf{b}}$ and $\bar{\mathbf{c}}$.

What has been shown above for central RSP–games can be applied to every RSP–game, since every RSP–game A can be *centralized*, i.e., transformed into a central RSP–game $A^{\boldsymbol{\pi}}$ by means of a barycentric transformation. In fact, $A^{\boldsymbol{\pi}}$ is a central game, if $\boldsymbol{\pi}$ is defined by

$$\pi_i := (p^*_i)^{-1}; \quad i \in I, \tag{5.35}$$

where $\mathbf{p}^*$ denotes the unique interior fixed point of A.

(3.18) and (5.27) imply that η and $\det(A_0)$ have the same sign for central games:

$$\operatorname{sgn}[\det(A_0)] = \operatorname{sgn}(\eta) = \operatorname{sgn}[\,\frac{\bar{b}+\bar{c}}{2} - \bar{a}\,]\,. \tag{5.36}$$

Correspondingly, the barycenter of a central game is hyperbolically stable if and only if $\det(A_0) > 0$. On the other hand, (5.15) shows that the sign of the determinant of an RSP–game is not changed by a barycentric transformation. Accordingly, the centralization of a given RSP–game and the application of Proposition 5.8 to it yields:

THEOREM 5.9: Hyperbolic stability in RSP–games.

Let A be an RSP–game, and let A_0 denote its interactive component. Then the following holds true:

1. The eigenvalues of the linearization at $\mathbf{p}^*$ are complex conjugate to one another.
2. The unique interior fixed point $\mathbf{p}^*$ of A is hyperbolically stable if and only if $\det(A_0) > 0$.
3. $\mathbf{p}^*$ is hyperbolically unstable if and only if $\det(A_0) < 0$.

Theorem 5.9 implies that a *Hopf bifurcation* (see, e.g., Marsden & McCracken 1976, Hassard, Kazarinoff & Wan 1981) occurs, whenever a change in one of the parameters of an RSP–game leads to a transition of the determinant of A_0 through zero (see, e.g., Figure 2). Theorem 5.6 shows that RSP–games do not admit *isolated* periodic orbits. This implies that the Hopf bifurcation necessarily is a *degenerate* one, since non–degenerate Hopf bifurcations imply the existence of an attracting or a repelling closed orbit (see, e.g., Marsden & McCracken 1976). The conclusion that RSP–games do not admit non–degenerate Hopf bifurcations for the continuous replicator dynamics does *not*, however, imply that RSP–games form a 'degenerate' class of evolutionary games. In fact, this phenonemon is typical for arbitrary evolutionary 3x3–games: Zeeman (1980) as well as Hofbauer (1981) have shown that *all* Hopf bifurcations are degenerate in the case $n = 3$. Isolated periodic orbits occur only in higher dimensions (i.e., $n \geq 4$).

6. Stability with Respect to the Discrete Replicator Dynamics

In this section, the stability of the interior fixed point $\mathbf{p}^*$ with respect to the discrete replicator dynamics (2.8) will be analysed. It will be shown that – like in the continuous time case – $\mathbf{p}^*$ is a global repellor if $\det(A_0)$, the determinant of the interactive component of A, is smaller than zero. In case that $\det(A_0) > 0$, however, the situation is different. In contrast to the continuous time case, stability of $\mathbf{p}^*$ can be affected by positive linear transformations of payoffs: $\mathbf{p}^*$ can always be stabilized *and* destablized with respect to (2.8) by means of a positive linear transformation of payoffs. In particular, this implies that evolutionary stability of $\mathbf{p}^*$ is neither necessary nor sufficient to ensure stability with respect to the discrete replicator dynamics.

The class of 'circulant' RSP–games will be analysed in some detail. For this class, the situation with respect to the discrete replicator dynamics is very similar to the picture that emerged for the continuous dynamics: local stability of the interior fixed point implies global hyperbolic stability, local instability implies global hyperbolic instability, and the parameter regions for stability and instability are separated by a submanifold of codimension one for which the interior fixed point is a global center.

To begin with, we shall give an equivalent representation of the discrete replicator equation (2.8) in terms of a *difference equation*:

$$\Delta\mathbf{p} := \mathbf{p}' - \mathbf{p} = \mathbf{w}^A(\mathbf{p}). \tag{6.1}$$

In this form, the discrete replicator dynamics is – like in the continuous case – induced by a vector field $\mathbf{w}^A\!: \Delta \longrightarrow \mathbb{R}^n_0$, the components of which are given by

$$w_i^A(\mathbf{p}) := p_i\,\frac{F_i(\mathbf{p}) - \bar{F}(\mathbf{p})}{\bar{F}(\mathbf{p})}, \quad i \in I. \tag{6.2}$$

A comparison of (6.2) with (5.2) shows that

$$\mathbf{w}^A(\mathbf{p}) := \frac{\mathbf{v}^A(\mathbf{p})}{\bar{F}(\mathbf{p})}. \tag{6.3}$$

Accordingly, the two vector fields $\mathbf{w}^A$ and $\mathbf{v}^A$ are collinear, and for each simplex point $\mathbf{p}$ the vectors $\mathbf{v}^A(\mathbf{p})$ and $\mathbf{w}^A(\mathbf{p})$ only differ in their lengths.

A simple calculation shows that (6.2) is 'well–behaved' with respect to barycentric transformations of the state space Δ: a barycentric transformation (5.12) of the strategy simplex transforms (6.2) into another discrete replicator dynamics, which is induced by the payoff matrix (5.13). Since every RSP–game can be centralized, i.e., transformed into a *central* RSP–game by means of a barycentric transformation of Δ, we shall restrict our attention to central games. Recall that an RSP–game is central if and only if its unique interior fixed point $\mathbf{p}^*$ coincides with the barycenter $\mathbf{m}$ of the simplex.

The *stability concepts* used in this section should be understood analogously to those used in the continuous case. The linearization of (6.1) at $\mathbf{p}^* = \mathbf{m}$ will be denoted by J_0:

$$J_0 := D\mathbf{w}^A(\mathbf{p}^*). \tag{6.4}$$

In view of (6.3) it is easy to see that $J_0 = D\mathbf{w}^A(\mathbf{p}^*)$ is related to $D = D\mathbf{v}^A(\mathbf{p}^*)$ by means of

$$J_0 = [\,\bar{F}(\mathbf{p}^*)\,]^{-1}\cdot D. \tag{6.5}$$

It is well–known that in the discrete case the stability behaviour of $\mathbf{p}^*$ is closely related to the spectral radius of the associated linear map

$$J_1 := J_0 + Id \tag{6.6}$$

(Id denotes the identity map). In fact, $\mathbf{p}^*$ is asymptotically stable, if all eigenvalues of J_1 have a modulus smaller than one, and it is unstable, if at least one eigenvalue of J_1 exceeds one in modulus. $\mathbf{p}^*$ is called *hyperbolically stable*, if all the eigenvalues of J_1 are located strictly within the unit circle, and it is called *hyperbolically unstable*, if at least one of the eigenvalues of J_1 has a modulus larger than one.

As described in Section 2., only non–negative fitness values make sense in the discrete generations context. Accordingly, the RSP–game $A = A(\mathbf{a},\mathbf{b},\mathbf{c})$ will be called *admissible* for the discrete replicator dynamics, if A is a non–negative matrix, i.e., if

$$b_i > a_i \geq c_i \geq 0 \quad \text{for } i \in I. \tag{6.7}$$

Let $A_0 = A(0,\beta,-\gamma)$ be an essential RSP–game, and let $\mathbf{a} \in \mathbb{R}^3$ denote a vector. If $\mathbf{a}$ is interpreted as the generating vector for the basic component A_1 of an RSP–game, the pair $(A_0,\mathbf{a})$ induces an RSP–game $A = A(A_0,\mathbf{a})$, which is given by

$$A(A_0,\mathbf{a}) := A_0 + A(\mathbf{a},\mathbf{a},\mathbf{a}). \tag{6.8}$$

The vector $\mathbf{a} \in \mathbb{R}^3$ will be called *admissible for* A_0, if $A(A_0,\mathbf{a})$ is an is admissible RSP–game for the discrete replicator dynamics. $\mathbf{a}$ is admissible for A_0 if and only if

$$\mathbf{a} \geq \gamma \geq \mathbf{0}, \tag{6.9}$$

where these vector inequalities should be understood component–wise.

Let now $A = A(\mathbf{a},\mathbf{b},\mathbf{c})$ be a central RSP–game, let J_0 denote the linearization of (6.1) at the interior fixed point $\mathbf{p}^* = \mathbf{m}$ of A, and let J_1 be given by (6.6). In view of Theorem 5.9(1) and (6.6), the eigenvalues of J_0 (and also those of J_1) are complex conjugate to one another. From this it is easy to derive (see Weissing 1983) that the interior fixed point is hyperbolically stable with respect to (6.1) if and only if the following inequality holds true:

$$\chi(\mathbf{p}^*) := \det(D) + \bar{F}(\mathbf{p}^*) \cdot \operatorname{tr}(D) < 0. \tag{6.10}$$

$\mathbf{p}^*$ is hyperbolically unstable, if and only if the inequality–sign in (6.10) is reversed.

It is clear that for any payoff matrix A, $\bar{F}(\mathbf{m})$ corresponds to the arithmetic mean of the entries of A. Together with (5.33) we get

$$\bar{F}(\mathbf{m}) = \tfrac{1}{3}\cdot(\bar{\mathbf{a}}+\bar{\mathbf{b}}+\bar{\mathbf{c}}) = \tfrac{1}{3}\cdot\eta + \bar{\mathbf{a}}. \tag{6.11}$$

Remember that $\operatorname{tr}(D)$ and $\det(D)$ are given by (5.29) and (5.30). Together with (6.11) and (5.33), this yields:

$$\chi(\mathbf{p}^*) = \tfrac{1}{3}\left[\, \tfrac{1}{3}\,\beta\cdot\gamma - \bar{\mathbf{a}}\,(\bar{\beta}-\bar{\gamma})\,\right]. \tag{6.12}$$

Combining all this, we have shown that:

<u>PROPOSITION 6.1:</u> Discrete hyperbolic stability in central RSP–games.

Let A be a central RSP–game and let $\mathbf{p}^* = \mathbf{m}$ denote its unique interior fixed point. Then the following holds true:

1. $\mathbf{p}^*$ is hyperbolically stable with respect to the discrete replicator equation (6.1) if and only if

$$\bar{\mathbf{a}}\,(\bar{\beta}-\bar{\gamma}) > \tfrac{1}{3}\,\beta\cdot\gamma. \tag{6.13}$$

2. $\mathbf{p}^*$ is hyperbolically unstable with respect to (6.1) if and only if

$$\bar{\mathbf{a}}\,(\bar{\beta}-\bar{\gamma}) < \tfrac{1}{3}\,\beta\cdot\gamma. \tag{6.14}$$

If $\bar{\beta}-\bar{\gamma} \leq 0$, we have $\bar{\mathbf{a}} \geq \bar{\gamma} \geq \bar{\beta} > 0$ and $\beta\cdot\gamma > 0$. In view of (6.14), this is sufficient to imply hyperbolical instability of the interior fixed point. If $\bar{\beta}-\bar{\gamma} > 0$, the interior fixed point is hyperbolically stable provided that $\bar{\mathbf{a}}$ is 'large enough'. It is clear that one can always achieve this by a positive linear transformation of payoffs. On the other hand, one can also almost always achieve hyperbolic instability by choosing $\bar{\mathbf{a}}$ 'small enough'. This will be shown next.

A simple calculation using the equalities $\beta_i = \eta + \gamma_{i+1}$, $i \in I$, yields

$$\tfrac{1}{3}\,\beta\cdot\gamma = \tfrac{1}{3}\sum_i \gamma_i\gamma_{i+1} + \eta\cdot\bar{\gamma}. \tag{6.15}$$

Together with (6.12) and $\eta = \bar{\beta}-\bar{\gamma}$, we get another formula for $\chi(\mathbf{p}^*)$:

$$\chi(\mathbf{p}^*) = \tfrac{1}{3}\left[\, \tfrac{1}{3}\sum_i \gamma_i\gamma_{i+1} - \eta\cdot(\bar{\mathbf{a}}-\bar{\gamma})\,\right]. \tag{6.16}$$

Remember that $\mathbf{p}^*$ is hyperbolically stable if and only if $\chi(\mathbf{p}^*) < 0$ and that it is hyperbolically unstable if and only if $\chi(\mathbf{p}^*) > 0$.

If $\eta = \bar{\beta} - \bar{\gamma} \leq 0$, we have $\gamma_{i+1} \geq \beta_i > 0, i \in I$. In view of $\bar{a} \geq \bar{\gamma}$, (6.16) implies that p^* is hyperbolically unstable since

$$\chi(p^*) \geq \tfrac{1}{9} \sum_i \beta_i \beta_{i+1} > 0, \quad \text{if } \eta \leq 0 . \tag{6.17}$$

Let us now analyse the case $\eta > 0$. (6.16) shows that p^* is hyperbolically stable if and only if

$$\bar{a} > \bar{\gamma} + \frac{1}{3 \cdot \eta} \cdot [\sum_i \gamma_i \gamma_{i+1}] . \tag{6.18}$$

p^* is hyperbolically unstable if and only if the inequality sign in (6.18) is reversed. (6.18) motivates the definition:

$$\varphi(A_0) := \frac{1}{3 \cdot \eta} \cdot [\sum_i \gamma_i \gamma_{i+1}], \quad \text{if } \eta > 0 . \tag{6.19}$$

If $\varphi(A_0) = 0$, p^* is hyperbolically stable if $\bar{a} > \bar{\gamma}$ and it is never hyperbolically unstable. Note that $\varphi(A_0) = 0$ if and only if at least two component of the vector γ are equal to zero. If $\varphi(A_0) > 0$, there are always admissible vectors a such that

$$\bar{\gamma} \leq \bar{a} < \bar{\gamma} + \varphi(A_0) , \tag{6.20}$$

i.e., such that p^* is hyperbolically unstable for the RSP–game $A = A(A_0, a)$. For example, the vector $a = \gamma$ is admissible for A_0, and p^* is hyperbolically unstable for the RSP–game $A(A_0, \gamma)$ if $\varphi(A_0) > 0$. On the other hand, the interior fixed point of $A = A(A_0, a)$ is hyperbolically stable if a is 'large enough' in the sense that

$$\bar{a} > \bar{\gamma} + \varphi(A_0). \tag{6.21}$$

Recall that for central RSP–games we have

$$\text{sgn}(\eta) = \text{sgn}[\det(A_0)] = \text{sgn}[\tfrac{1}{2} \cdot (\bar{b} + \bar{c}) - \bar{a}]. \tag{6.22}$$

Together with the above observations we get:

COROLLARY 6.2: Discrete hyperbolic instability in central RSP–games.

Let $A = A(a,b,c) = A(A_0, a)$ be a central RSP–game and let $p^* = m$.

1. If $\det(A_0) \leq 0$, p^* is hyperbolically unstable with respect to the discrete replicator dynamics (6.1) irrespective of the vector a.
2. If $\det(A_0) > 0$ and $\varphi(A_0) = 0$, p^* is hyperbolically stable with respect to the discrete replicator dynamics if and only if $a \geq \gamma$, $a \neq \gamma$.
3. If $\det(A_0) > 0$ and $\varphi(A_0) > 0$, p^* is hyperbolically unstable with respect to (6.1) if and only if (6.20) holds true. In particular, it is hyperbolically unstable for $a = \gamma$. On the other hand, p^* is hyperbolically stable if a is large enough in the sense that (6.21) holds true.

All these results can easily be generalized to non–central RSP–games. In fact, every RSP–game $A = A(a,b,c) = A(A_0, a)$ with interior fixed point p^* can be centralized by a barycentric transformation, the generating vector π of which is given by (5.35). It is obvious that A is transformed into the central RSP–game

$$A^\pi = A(a^\pi, b^\pi, c^\pi) = A((A_0)^\pi, a^\pi) , \tag{6.23}$$

where a^π, b^π, c^π and $(A_0)^\pi$ are given by

$$a_j^\pi := a_j \cdot p_j^* , \; b_j^\pi := b_j \cdot p_j^* , \; c_j^\pi := c_j \cdot p_j^* , \tag{6.24}$$

$$\beta_j^\pi := \beta_j \cdot p_j^* , \; \gamma_j^\pi := \gamma_j \cdot p_j^* . \tag{6.25}$$

Notice that $\text{sgn}[\det(A_0{}^\pi)] = \text{sgn}[\det(A_0)]$, that a^π can be made arbitrarily large by increasing a, and that $\sum_i \gamma_i^\pi \gamma_{i+1}^\pi = 0$ is equivalent to $\sum_i \gamma_i \gamma_{i+1} = 0$. From this we get:

THEOREM 6.3: Discrete hyperbolic stability in RSP–games.

Let A_0 be an RSP–game in essential form, and let p^* denote its interior fixed point.

1. If $\det(A_0) \leq 0$, p^* is hyperbolically unstable with respect to the discrete replicator dynamics for all RSP–games that have A_0 as their interactive component.
2. If $\det(A_0) > 0$ and $\sum_i \gamma_i \gamma_{i+1} = 0$, p^* is hyperbolically stable for all RSP–games $A(A_0, a)$ with $a \geq \gamma$, $a \neq \gamma$.
3. If $\det(A_0) > 0$ and $\sum_i \gamma_i \gamma_{i+1} > 0$, there exists a real number $\psi(A_0) > \gamma \cdot p^* \geq 0$ such that p^* is hyperbolically unstable for all admissible RSP–games $A(A_0, a)$ with $a \cdot p^* < \psi(A_0)$ and hyperbolically stable for all $A(A_0, a)$ with $a \cdot p^* > \psi(A_0)$.

The two main conclusions of Theorem 6.3 will be stated as a corollary:

COROLLARY 6.4: Evolutionary stability and discrete dynamic stability.

1. The concept of *discrete stability*, i.e., stability with respect to (6.1), is *not* invariant with respect to positive linear transformations of the payoff matrix.
2. Evolutionary stability is neither necessary nor sufficient for discrete stability. In fact, an ESS may be hyperbolically unstable with respect to (6.1), and a hyperbolic attractor with respect to (6.1) need not be an ESS.

The potential discrete instability of an evolutionarily stable strategy is illustrated in Figure 4. An orbit starting at $p_0 = (0.25, 0.25, 0.5)$ is shown there for (a) the discrete replicator dynamics and a small value of $\bar{a}$, (b) the discrete replicaotr dynamics and a large value of $\bar{a}$, and (c) the continuous replicator dynamics.

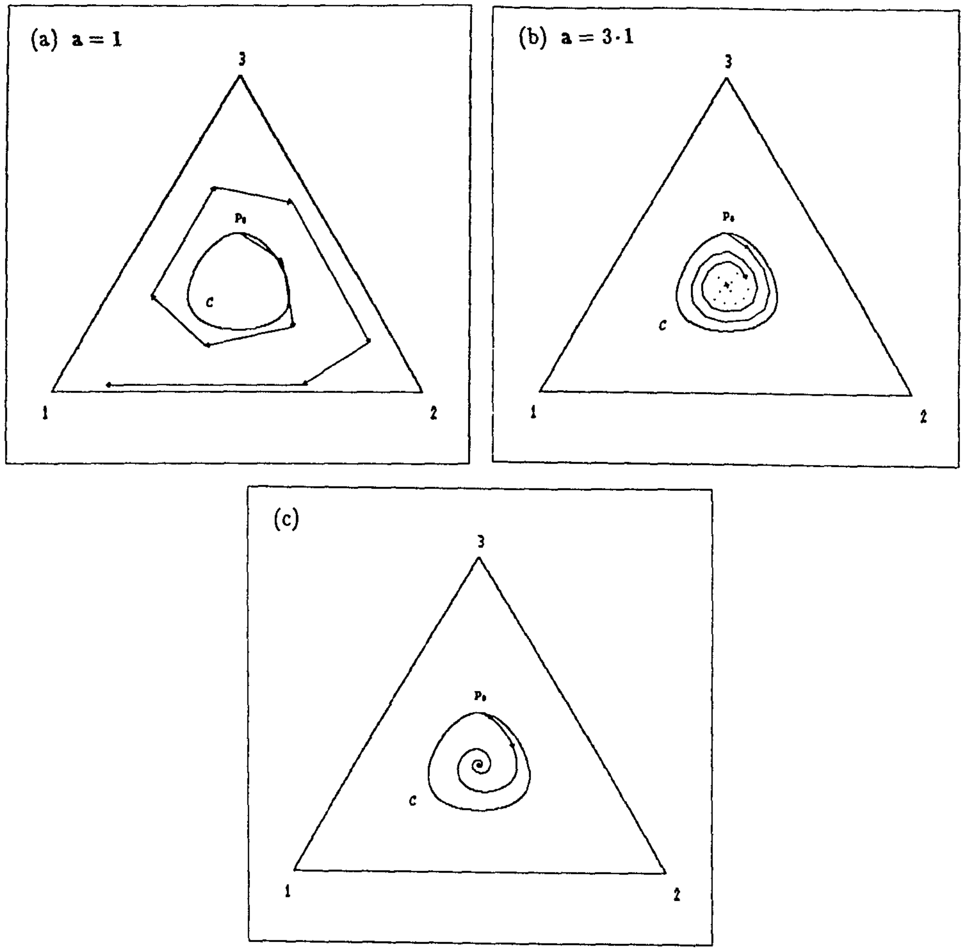


FIGURE 4: Discrete dynamic instability of an evolutionarily stable strategy. Figure 4 is based on the central RSP–game $A = A(A_0,\mathbf{a})$, where:

$$A_0 = \begin{bmatrix} 0 & 2 & -1 \\ -1 & 0 & 2 \\ 2 & -1 & 0 \end{bmatrix} \quad \text{and} \quad \mathbf{a} = \lambda\cdot\gamma = \lambda\cdot 1.$$

C is a constant–level curve of the scalar function V (see (5.5)); the initial vector $\mathbf{p}_0 := (0.25, 0.25, 0.5)$ belongs to C.

(a) $\mathbf{a} = \gamma$: $\mathbf{p}^*$ is hyperbolically *unstable* with respect to (6.1). The vector attached to $\mathbf{p}_0$ is so large that it 'overshoots' C.

(b) $\mathbf{a} = 3\gamma$: $\mathbf{p}^*$ is hyperbolically *stable* with respect to (6.1). Overshooting does not occur.

(c) Orbit of the *continuous* replicator dynamics starting at $\mathbf{p}_0$.

Figure 4 is based on an ϵ–perturbed Rock–Scissors–Paper game with $\epsilon > 0$. As has been shown in Section 5, the interior fixed point $\mathbf{p}^* = \mathbf{m}$ is an ESS and a global attractor with respect to the continuous replicator dynamics. The initial vector $\mathbf{p}_0$ belongs to the closed curve C, which is a constant–level curve of the scalar function V that was defined in (5.5). Since $\mathbf{p}^*$ is an ESS, V is a global Lyapunov function for the continuous replicator dynamics.

By definition, this means that the trajectories of (5.1) cross constant–level curves like C from the outside to the inside with respect to C. Equivalently, the vectors of the vector field $\mathbf{v}^A$ point 'inward' for all points on C. Since the vector field $\mathbf{w}^A$ of the discrete replicator dynamics is collinear to $\mathbf{v}^A$, the vectors $\mathbf{w}^A(\mathbf{p})$ also point inward when attached to points $\mathbf{p}$ on C. However, in view of (6.3) and (6.11), the length of a vector $\mathbf{w}^A(\mathbf{p})$ is negatively correlated with $\bar{\mathbf{a}}$. For small values of $\bar{\mathbf{a}}$, the length of $\mathbf{w}^A(\mathbf{p})$ may be so large that $\mathbf{p}' = \mathbf{p} + \mathbf{w}^A(\mathbf{p})$ lies outside the closed curve C (see Figure 4(a)). *Overshootings* like this, which are closely connected with the value of $\bar{\mathbf{a}}$ (see Figure 4(b)), are the reasons for the potential instability of an ESS with respect to the discrete replicator dynamics.

Theorem 6.3 indicates that for $\det(A_0) > 0$ we can always find an $\mathbf{a}$ that is large enough to prevent overshootings. (In Weissing (1990), this result is generalized to the class of all evolutionary normal form games.) On the other hand – neglecting the border case $\sum_i \gamma_i\gamma_{i+1} = 0$ – overshootings leading to instability do *always* occur if the vector $\mathbf{a}$ is not significantly larger than γ.

In Section 5. we saw that for the continuous replicator dynamics the *local* stability properties of the interior fixed point of an RSP–game correspond perfectly to *global* stability properties. We shall now turn to this question for the case of the discrete replicator dynamics (6.1).

Again, global stability properties will be analysed by constructing suitable Lyapunov functions for (6.1). As in the continuous time case, a *Lyapunov function* is a scalar function $W: \Delta \to \mathbb{R}$, which has a strict local maximum in $\mathbf{p}^*$ and which changes in a definite way along the orbits of the dynamical system. The last condition means that the change along orbits, ∇W, should either be positive near $\mathbf{p}^*$, or negative near $\mathbf{p}^*$, or identical to zero near $\mathbf{p}^*$. ∇W is defined by

$$\nabla W(\mathbf{p}) := W(\mathbf{p}') - W(\mathbf{p})\,. \tag{6.26}$$

The 'standard' Lyapunov function $V: \Delta \to \mathbb{R}$ for the continuous replicator dynamics – which is given by (5.5) – is also very useful in the context of the discrete replicator equation. In fact, V can always be used for demonstrating discrete instability of $\mathbf{p}^*$, if $\mathbf{p}^*$ is uniformly evolutionarily unstable. On the other hand, V is a global discrete Lyapunov function whenever $\mathbf{p}^*$ is an ESS and the vector $\mathbf{a}$ is 'large enough' to prevent overshootings. These results – which hold true for general evolutionary normal form games – are derived in Weissing (1990). The following theorem combines those results in Weissing (1990) which are relevant for RSP–games:

THEOREM 6.5: Evolutionary stability and global discrete stability.

Let $\mathbf{p}^*$ denote an interior Nash strategy of an evolutionary normal form game A_0. Then the following holds true:

1. If $\mathbf{p}^*$ is the unique interior Nash strategy, and if $\mathbf{p}^*$ is uniformly evolutionarily unstable, it is a global repellor for the discrete replicator dynamics for all games $A = (A_0,\mathbf{a})$ such that the vector $\mathbf{a}$ is admissible for A_0.
2. If $\mathbf{p}^*$ is an ESS, there exists an admissible vector $\mathbf{a}^+$ such that $\mathbf{p}^*$ is a global attractor for the discrete replicator dynamics for all games $A = (A_0,\mathbf{a})$ with $\mathbf{a} \geq \mathbf{a}^+$.

Theorem 6.5 directly applies to the class of balanced RSP–games, since the interior fixed point of a balanced RSP–game is always either an ESS or uniformly evolutionarily unstable (Proposition 5.3). On the other hand, every RSP–game can be transformed into a balanced one by means of a barycentric transformation of the state space (Theorem 5.5), and barycentric transformations do not change the dynamic features of the discrete replicator dynamics. Consequently, Theorem 6.5 yields:

THEOREM 6.6: Discrete global stability in RSP–games.

Let A_0 be an RSP–game in essential form, and let $\mathbf{p}^*$ denote its interior fixed point.

1. If $\det(A_0) \leq 0$, $\mathbf{p}^*$ is a global hyperbolic repellor with respect to the discrete replicator dynamics for any RSP–game $A = A(A_0,\mathbf{a})$ the interactive component ofwhich is given by A_0.
2. If $\det(A_0) > 0$, there exists an admissible vector $\mathbf{a}^+ \in \mathbb{R}^3$ for A_0 such that $\mathbf{p}^*$ is a global hyperbolic attractor with respect to the discrete replicator dynamics for all RSP–games $A(A_0,\mathbf{a})$ with $\mathbf{a} \geq \mathbf{a}^+$.

The example in Figure 4 shows that even for an ESS of a perfectly balanced, central RSP–game the function V is in general not a discrete Lyapunov function. There is, however, a class of RSP–games which is so simple in structure that a global discrete Lyapunov function can be found for all parameter constellations. It is the class of 'circulant' RSP–games, the properties of which will be analysed next.

An RSP–game $A = A(\mathbf{a},\mathbf{b},\mathbf{c})$ will be called a *circulant RSP–game* if the vectors $\mathbf{a}$, $\mathbf{b}$, and $\mathbf{c}$ are all scalar multiples of the vector $\mathbf{1}$. Accordingly, an RSP–game is circulant if and only if its payoff matrix is a 'circulant matrix' (see, e.g., Davis 1979), i.e., if A is of the form

$$A = \begin{bmatrix} a & b & c \\ c & a & b \\ b & c & a \end{bmatrix}, \quad b > a \geq c\,. \tag{6.27}$$

It is clear that circulant RSP–games are central, perfectly balanced games, and that the class of these games includes the ϵ–perturbed Rock–Scissors–Paper games which are defined by (1.4). Setting

$$\beta := b-a, \quad \gamma := a-c, \quad \text{and} \quad \delta := \beta-\gamma\,, \tag{6.28}$$

we get from (6.22):

$$\operatorname{sgn}[\,\det(A_0)\,] = \operatorname{sgn}(\delta) = \operatorname{sgn}[\,\tfrac{b+c}{2} - a\,]\,. \tag{6.29}$$

On the other hand, a simple calculation based on (6.12) shows that $\chi(\mathbf{p}^*)$ is given by

$$\chi(\mathbf{p}^*) = \tfrac{1}{3}[\,a^2 - bc\,]\,. \tag{6.30}$$

Now Theorem 5.3, Theorem 6.1, and Theorem 6.6 taken together provide a nice characterization of evolutionary stability and dynamic stability in circulant RSP–games:

COROLLARY 6.7: Stability in circulant RSP–games.

Let A denote a circulant RSP–game given by (6.27). Then the following holds true:

1. The interior Nash strategy $\mathbf{p}^* = \mathbf{m}$ is an ESS if and only if
$$a < (b+c)/2\,, \tag{6.31}$$
i.e., if and only if a is smaller than the arithmetic mean of b and c.
2. $\mathbf{p}^*$ is a global hyperbolic attractor with respect to the continuous replicator dynamics if and only if (6.31) holds true. It is a global center if $a = (b+c)/2$, and it is a global hyperbolic repellor if $a > (b+c)/2$.
3. $\mathbf{p}^*$ is hyperbolically stable with respect to the discrete replicator dynamics (6.1) if and only if
$$a^2 < bc, \tag{6.32}$$
i.e., if a is smaller than the geometric mean of b and c.
$\mathbf{p}^*$ is hyperbolically unstable if and only if $a^2 > bc$. If $a \geq (b+c)/2$, it is a *global* hyperbolic repellor for the discrete replicator dynamics.

For circulant RSP–games, it is the inequality between the arithmetic and the geometric mean which leaves room for a discrepancy between 'discrete' and 'continuous' stability to occur. In fact, the interior fixed point is a hyperbolic *attractor* for the continuous replicator dynamics and at the same time a hyperbolic *repellor* for the discrete replicator equation if

$$\sqrt{bc} < a < \tfrac{b+c}{2}\,. \tag{6.33}$$

We shall now prove a theorem which shows that for *circulant* RSP–games there is a perfect correspondence between local discrete stability and global discrete stability:

<u>THEOREM 6.8:</u> Global discrete stability in circulant RSP–games.

Let A denote a circulant RSP–game given by (6.27). Let $\mathbf{p}^* = \mathbf{m}$ denote its interior fixed point. Then the following holds true:

1. If $a^2 < bc$, $\mathbf{p}^*$ is a global hyperbolic attractor for the discrete replicator dynamics.
2. If $a^2 > bc$, $\mathbf{p}^*$ is a global hyperbolic repellor for (6.1).
3. If $a^2 = bc$, $\mathbf{p}^*$ is a global center for (6.1), i.e., the interior of the strategy simplex is filled with closed invariant curves encircling $\mathbf{p}^*$.

Figure 5 illustrates how the phase portrait of the discrete replicator dynamics changes near $a = \sqrt{bc}$. In (c), each orbit is iterated for only about 100 generations. Obviously, each of the closed invariant curves surrounding $\mathbf{p}^*$ consists of many orbits of (6.1), since each orbit has only a countable number of elements. In my numerical simulations, I have never observed a finite non–equilibrium orbit corresponding to a periodic trajectory. Instead, the simulations suggest that each orbit is dense on the closed invariant curve to which it belongs.

<u>PROOF of THEOREM 6.8:</u>

A: In view of Corollary 6.7.3, we may concentrate on the case $a < (b+c)/2$. We shall therefore assume that (6.31) holds true and that the interior fixed point $\mathbf{p}^* = \mathbf{m}$ isan ESS of A.

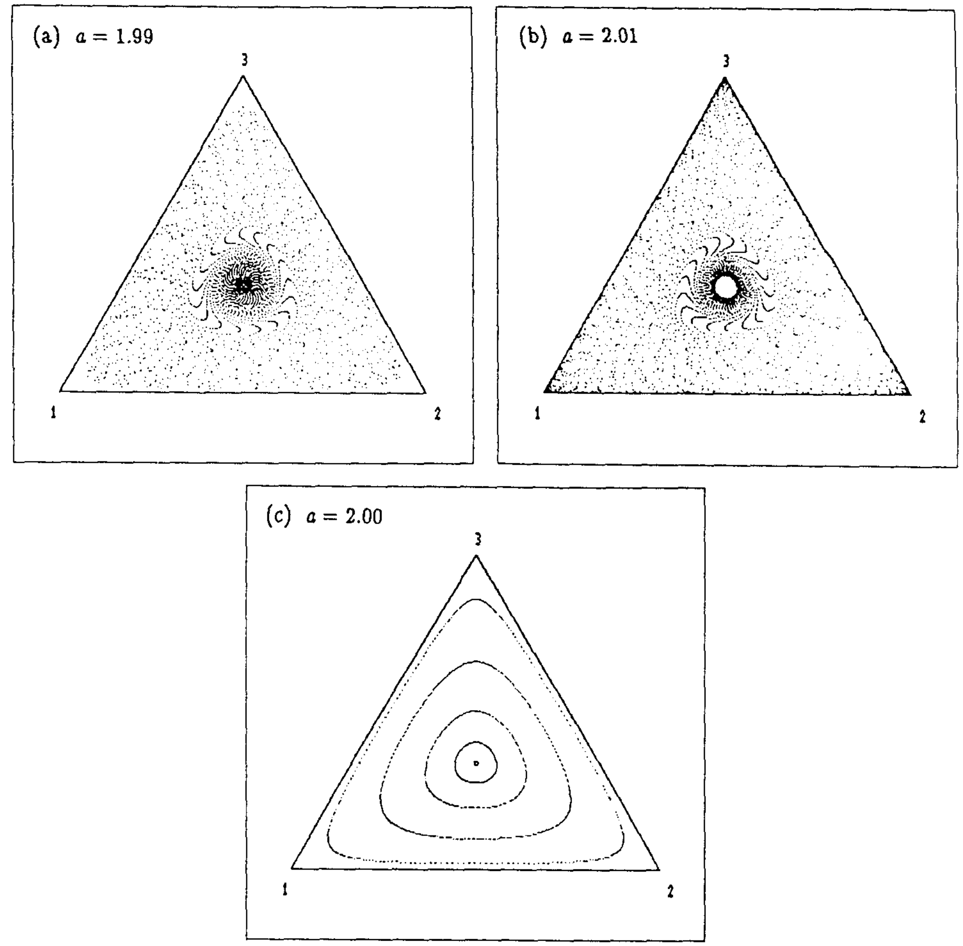
Theorem 6.8 will be proved by constructing a suitable global Lyapunov function for (6.1). We shall consider the scalar function $W\colon \mathrm{int}(\Delta) \longrightarrow \mathbb{R}$, which is defined by

$$W(\mathbf{q}) := \frac{\mathbf{q}\cdot A\mathbf{q}}{q_1 q_2 q_3}, \quad \mathbf{q} \in \mathrm{int}(\Delta)\,. \tag{6.34}$$

(Josef Hofbauer and Karl Sigmund directed my attention to this function.) It will be shown that the interior fixed point $\mathbf{p}^* = \mathbf{m}$ of A is the only critical point of W, and that it is a strict global minimum of W. Moreover, ∇W has a definite sign along the orbits of the discrete replicator dynamics (6.1). In fact, we shall show that the sign of $\nabla W(\mathbf{q})$ is independent of $\mathbf{q}$, and that it is given by

$$\mathrm{sgn}[\nabla W(\mathbf{q})] = \mathrm{sgn}[a^2 - bc]\,. \tag{6.35}$$

Accordingly, W increases along the orbits of (6.1) if and only if $a^2 > bc$; W decreases along the orbits of (6.1) iff $a^2 < bc$; and it is a constant of motion if and only if $a^2 = bc$. The assertions of Theorem 6.8 follow immediately from these properties.



<u>FIGURE 5:</u> Discrete dynamic stability in a family of circulant RSP–games:

$$A(a) == \begin{bmatrix} a & 4 & 1 \\ 1 & a & 4 \\ 4 & 1 & a \end{bmatrix}, \quad 4 > a \geq 1\,.$$

(a) $a < \sqrt{bc}$: $\mathbf{p}^*$ is a global hyperbolic attractor.
The diagram shows the orbit starting at $\mathbf{p}_0 := (0.05,0.05,0.90)$.

(b) $a > \sqrt{bc}$: $\mathbf{p}^*$ is a global hyperbolic repellor.
The diagram shows the orbit starting at $\mathbf{p}_0 := (0.35,0.35,0.30)$.

(c) $a = \sqrt{bc}$: $\mathbf{p}^*$ is a global center. Five orbits are shown which indicate the closed invariant curves encircling $\mathbf{p}^*$.

B: First, we shall show that W has a global minimum in $\mathbf{p}^*$. A simple calculation yields that $\mathbf{q}\cdot A\mathbf{q}$ may be represented in the form

$$\mathbf{q}\cdot A\mathbf{q} = a + (b+c-2a)(q_1q_2 + q_2q_3 + q_3q_1). \tag{6.36}$$

Therefore, $W(\mathbf{q})$ may be written as

$$W(\mathbf{q}) = a\cdot\frac{1}{q_1q_2q_3} + (b+c-2a)\cdot(\frac{1}{q_1} + \frac{1}{q_2} + \frac{1}{q_3}). \tag{6.37}$$

In view of (6.27) and (6.31) this shows that W is a positive linear combination of the two scalar functions W_1 and W_2, which are given by

$$W_1(\mathbf{q}) := \frac{1}{q_1q_2q_3} \quad\text{and}\quad W_2(\mathbf{q}) := \frac{1}{q_1} + \frac{1}{q_2} + \frac{1}{q_3}. \tag{6.38}$$

Notice that $W_1(\mathbf{q})$ is the inverse of the third power of the geometric mean of $\mathbf{q}$, whereas $W_2(\mathbf{q})$ is the inverse of the harmonic mean of $\mathbf{q}$. It is well-known that the geometric as well as the harmonic mean have a strict global maximum in the barycenter $\mathbf{m}$ of the simplex. Correspondingly, W_1 and W_2 both h ve a strict global minimum in $\mathbf{m}$. Being a positive linearcombination of W_1 and W_2, W also has a strict global minimum in $\mathbf{p}^* = \mathbf{m}$.

C: We shall use the method of Lagrange multipliers in order to show that $\mathbf{p}^*$ is the only critical point of W. Therefore, we consider the term

$$\frac{\partial}{\partial q_i}[W(\mathbf{q}) - \lambda \sum_i q_i] = -\frac{1}{q_i}[a\, W_1(\mathbf{q}) + (b+c-2a)\,\frac{1}{q_i}] - \lambda\,, \tag{6.39}$$

where λ denotes a Lagrange mulitplier. Setting (6.39) equal to zero for $i \in I$, we get

$$\lambda = \lambda \sum_i q_i = -[W(\mathbf{q}) + 2a\, W_1(\mathbf{q})] \tag{6.40}$$

and

$$a\cdot W_1(\mathbf{q})\cdot(1-3q_i) = (b+c-2a)\cdot q_i\cdot[W_2(\mathbf{q}) - (q_i)^{-2}]\,. \tag{6.41}$$

Let us assume that $\mathbf{q} \neq \mathbf{m}$ and that i minimizes q_i. Then we have $q_i < 1/3$ and $W_2(\mathbf{q}) < 3/q_i$ which implies

$$W_2(\mathbf{q}) - (q_i)^{-2} < \frac{1}{q_i}\cdot(3 - \frac{1}{q_i}) < 0. \tag{6.41a}$$

Therefore the right-hand side of (6.41) is negative whereas the left-hand side is negative. This contradiction shows that (6.41) is only compatible with $\mathbf{q} = \mathbf{m}$: $\mathbf{p}^* = \mathbf{m}$ is the only critical point of W in $\mathrm{int}(\Delta)$.

D: In order to prove (6.35), we shall first derive an indicator function for the sign of ∇W. Let us define two auxiliary functions $M: \mathbb{R}^3 \to \mathbb{R}$ and $P: \mathbb{R}^3 \to \mathbb{R}$ by

$$M(\mathbf{z}) := \mathbf{z}\cdot A\mathbf{z},\quad P(\mathbf{z}) := z_1z_2z_3,\quad \mathbf{z} \in \mathbb{R}^n. \tag{6.42}$$

Using these functions, $W(\mathbf{q})$ may be written as

$$W(\mathbf{q}) = \frac{M(\mathbf{q})}{P(\mathbf{q})},\quad \mathbf{q} \in \mathrm{int}(\Delta)\,. \tag{6.43}$$

Let us now choose a fixed strategy $\mathbf{q} \in \mathrm{int}(\Delta)$, $\mathbf{q} \neq \mathbf{m}$. Denote the fitness vector at $\mathbf{q}$ by $\mathbf{y} \in \mathbb{R}^3$, i.e.,

$$\mathbf{y} := F(\mathbf{q}) = A\mathbf{q}\,. \tag{6.44}$$

From the definition (2.8) of $\mathbf{q}'$ we get

$$P(\mathbf{q}') = P(\mathbf{q})\cdot\frac{P(\mathbf{y})}{(M(\mathbf{q}))^3}\,. \tag{6.45}$$

This implies

$$W(\mathbf{q}') = \frac{M(\mathbf{q}')}{P(\mathbf{q}')} = W(\mathbf{q})\cdot\frac{M(\mathbf{q}')(M(\mathbf{q}))^2}{P(\mathbf{y})}\,, \tag{6.46}$$

and

$$\nabla W(\mathbf{q}) := W(\mathbf{q}')-W(\mathbf{q}) = \frac{W(\mathbf{q})}{P(\mathbf{y})}\cdot[\,M(\mathbf{q}')(M(\mathbf{q}))^2 - P(\mathbf{y})\,]\,. \tag{6.47}$$

A few simple calculations yield

$$M(\mathbf{q}')\cdot[M(\mathbf{q})]^2 = \Psi(\mathbf{q})\,, \tag{6.48}$$

where $\Psi(\mathbf{q})$ is given by

$$\Psi(\mathbf{q}) := a(\sum_i q_i^2y_i^2) + (b+c)(\sum_i q_iq_{i+1}y_iy_{i+1})\,. \tag{6.49}$$

Combining (6.47) and (6.48), we get:

$$\mathrm{sgn}[\nabla W(\mathbf{q})] = \mathrm{sgn}[\Psi(\mathbf{q})-P(\mathbf{y})]\,. \tag{6.50}$$

E: We shall now derive an explicit representation of the expression $\Psi(\mathbf{q})-P(\mathbf{y})$. The following identities will be used:

$$\sum_i q_i^2q_{i+1}^2 = \sum_i q_i^2q_{i+2}^2\,, \tag{6.51}$$

$$\sum_i q_i^3q_{i+2} = \sum_i q_iq_{i+1}^3\,, \tag{6.52}$$

$$q_1q_2q_3 = \sum_i q_i^2q_{i+1}q_{i+2} = \sum_i q_iq_{i+1}^2q_{i+2} = \sum_i q_iq_{i+1}q_{i+2}^2, \tag{6.53}$$

$$\sum_i q_i^3 = \sum_i q_i^4 + \sum_i q_i^3q_{i+1} + \sum_i q_iq_{i+1}^3\,, \tag{6.54}$$

$$\sum_i q_i^2q_{i+1} = \sum_i q_i^2q_{i+1}^2 + \sum_i q_i^3q_{i+1} + q_1q_2q_3\,, \tag{6.55}$$

$$\sum_i q_iq_{i+1}^2 = \sum_i q_i^2q_{i+1}^2 + \sum_i q_iq_{i+1}^3 + q_1q_2q_3\,. \tag{6.56}$$

(6.51), (6.52), and the last two equalities in (6.53) are consequences of the fact that pure strategies are counted modulo three. The other equalities result by multiplying the left hand sides by the factor $\sum_i q_i$ (which is equal to one). Using (6.51) to (6.56), it is easy to derive the following formulae:

$$\begin{aligned}
\sum_i q_i^2 y_i^2 &= \sum_i q_i^2\cdot(aq_i+bq_{i+1}+cq_{i+2})^2 \\
&= a^2\cdot(\sum_i q_i^4) + (b^2+c^2)\cdot(\sum_i q_i^2 q_{i+1}^2) + \qquad (6.57)\\
&\quad + 2ab\cdot(\sum_i q_i^3 q_{i+1}) + 2ac\cdot(\sum_i q_i q_{i+1}^3) + 2bc\cdot q_1q_2q_3\,,
\end{aligned}$$

$$\begin{aligned}
\sum_i q_i q_{i+1} y_i y_{i+1} &= \sum_i q_i q_{i+1}\cdot(aq_i+bq_{i+1}+cq_{i+2})\cdot(aq_{i+1}+bq_{i+2}+cq_i) \\
&= (a^2+bc)\cdot(\sum_i q_i^2 q_{i+1}^2) + ac\cdot(\sum_i q_i^3 q_{i+1}) + \qquad (6.58)\\
&\quad + ab\cdot(\sum_i q_i q_{i+1}^3) + (b^2+c^2+ab+ac+bc)\cdot q_1q_2q_3\,,
\end{aligned}$$

$$\begin{aligned}
P(y) &= (aq_i+bq_{i+1}+cq_{i+2})\cdot(aq_{i+1}+bq_{i+2}+cq_i)\cdot(aq_{i+2}+bq_i+cq_{i+1}) \\
&= abc\cdot(\sum_i q_i^3) + (a^2b+b^2c+c^2a)\cdot(\sum_i q_i^2 q_{i+1}) + \\
&\quad + (a^2c+b^2a+c^2b)\cdot(\sum_i q_i q_{i+1}^2) + (a^3+b^3+c^3+3abc)\cdot q_1q_2q_3 \\
&= abc\cdot(\sum_i q_i^4) + \\
&\quad + (a^2b+b^2c+c^2a+a^2c+b^2a+c^2b)\cdot(\sum_i q_i^2 q_{i+1}^2) + \\
&\quad + (abc+a^2b+b^2c+c^2a)\cdot(\sum_i q_i^3 q_{i+1}) + \qquad (6.59)\\
&\quad + (abc+a^2c+b^2a+c^2b)\cdot(\sum_i q_i q_{i+1}^3) + \\
&\quad + (a^3+b^3+c^3+3abc+a^2b+b^2c+c^2a+a^2c+b^2a+c^2b)\cdot q_1q_2q_3
\end{aligned}$$

Combining (6.57), (6.58), and (6.59), we get that $\Psi(q)-P(y)$ is of the form:

$$\begin{aligned}
\Psi(q)-P(y) &= \sigma_4\cdot(\sum_i q_i^4) + \sigma_3\cdot(\sum_i q_i^3 q_{i+1}^1) + \sigma_2\cdot(\sum_i q_i^2 q_{i+1}^2) + \\
&\quad + \sigma_1\cdot(\sum_i q_i q_{i+1}^3) + \sigma_0\cdot q_1q_2q_3, \qquad (6.60)
\end{aligned}$$

where the coefficients σ_i are given by

$$\sigma_4 = a^3 - abc = a\cdot(a^2-bc), \qquad (6.61)$$

$$\sigma_3 = 2a^2b + (b+c)\cdot ac - (abc+a^2b+b^2c+c^2a) = b\cdot(a^2-bc), \qquad (6.62)$$

$$\sigma_2 = a\cdot(b^2+c^2) + (b+c)\cdot(a^2+bc) - (a^2b+b^2c+c^2a+a^2c+b^2a+c^2b) = 0, \qquad (6.63)$$

$$\sigma_1 = 2a^2c + (b+c)\cdot ab - (abc+a^2c+b^2a+c^2b) = c\cdot(a^2-bc), \qquad (6.64)$$

$$\begin{aligned}
\sigma_0 &= 2abc + (b+c)\cdot(b^2+c^2+ab+bc+ca) - (a^3+b^3+c^3+3abc+(b+c)(a^2+bc)+ab^2+ac^2) \\
&= abc + bc^2 + b^2c - a^3 - a^2b - a^2c = -(a+b+c)\cdot(a^2-bc). \qquad (6.65)
\end{aligned}$$

F: On the basis of (6.61) to (6.65), it is easy to see that $\Psi(q)-P(y)$ may be put into the form

$$\Psi(q) - P(y) = (a^2-bc)(\, a\cdot\Phi_1(q) + b\cdot\Phi_2(q) + c\cdot\Phi_3(q)\,), \qquad (6.66)$$

where the functions $\Phi_i(q)$ are given by

$$\Phi_1(q) := (\sum_i q_i^4) - q_1q_2q_3, \qquad (6.67)$$

$$\Phi_2(q) := (\sum_i q_i^3 q_{i+1}) - q_1q_2q_3, \qquad (6.68)$$

$$\Phi_3(q) := (\sum_i q_i q_{i+1}^3) - q_1q_2q_3. \qquad (6.69)$$

We want to show that

$$\operatorname{sgn}[\nabla W(q)] = \operatorname{sgn}[\Psi(q)-P(y)] = \operatorname{sgn}[a^2-bc] \qquad (6.70)$$

for all $q \neq m$. In view of (6.50) and (6.66), (6.70) is a consequence of

$$\Phi_i(q) > 0 \quad \text{for } i \in I \text{ and } q \neq m. \qquad (6.71)$$

The proof of Theorem 6.8 will be completed by showing that (6.71) holds true.

G: Let us first show that $\Phi_1(q) > 0$ holds true for $q \neq m$: Jensen's inequality applied to the convex function $f(y) := y^4$ yields for $n = 3$:

$$\sum_i q_i^4 \geq n\cdot(\sum_i \frac{1}{n}\, q_i)^4 = \frac{1}{27}\cdot(\sum_i q_i)^4 = \frac{1}{27}, \qquad (6.72)$$

with equality only for $q = m$. On the other hand, we have

$$q_1q_2q_3 = P(q) \leq P(m) = \frac{1}{27}, \qquad (6.73)$$

with equality only for $q = m$. Taken together, (6.72) and (6.73) yield (6.71) for $i = 1$. Considering $i = 2$, a simple calculation using (6.55) shows that

$$\Phi_2(q) = (\sum_i q_i^2 q_{i+1}) - (\sum_i q_i q_{i+1})^2. \qquad (6.74)$$

Jensen's inequality applied to the convex function $f(y) := y^2$ yields (6.71) for $i = 2$. The corresponding result for $i = 3$ follows immediately in view of the symmetry of the expressions (6.68) and (6.69).

This completes the proof of Theorem 6.8. * * *

7. Complex Attractors of the Discrete Replicator Dynamics

In the last section we saw that for *circulant* RSP–games the dynamical features with respect to the discrete replicator equation are 'qualitatively' closely analogous to those obtained for the continuous replicator dynamics. In both cases there are only three types of global dynamic behaviour: the interior fixed point p^* is either a global attractor, or a global repellor, or a global center. For the discrete as well as for the continuous dynamics, the parameter region $\mathcal{P}_0$ for which p^* is a center is a submanifold of codimension one in parameter space which separates the parameter regimes for stability and instability. Whenever $\mathcal{P}_0$ is crossed transversally by a one–parameter family of circulant RSP–games, a Hopf bifurcation does occur which is *degenerate* (see below) since the games in $\mathcal{P}_0$ do not admit *isolated* closed invariant curves encircling the interior fixed point. For circulant RSP–games, the main difference between the discrete and the continuous replicator dynamics is a quantitative one in that the stability of the interior fixed point changes at different parameter constellations for the two dynamics: at $\mathcal{P}_0 = \{ (a,b,c) \mid a = \sqrt{bc} \}$ for the discrete dynamics, and at $\mathcal{P}_0 = \{ (a,b,c) \mid a = (b+c)/2 \}$ for the continuous replicator equation.

In this section, we shall demonstrate that the perfect qualitative correspondence between the continuous and the discrete replicator dynamics does not extend to the class of all RSP–games. This is illustrated by an example in Figure 6. In that example, the interior fixed point is locally hyperbolically unstable with respect to the discrete replicator dynamics, but it is not a *global* repellor. Instead, there exists an invariant simple closed curve $\mathcal{C}$ encircling the interior fixed point which attracts all interior non–equilibrium orbits. $\mathcal{C}$ as well as the region enclosed by it are invariant sets for the discrete replicator equation. This phenonemon will be analysed more closely in the present section.

A simple closed curve which is invariant and attractive (or repulsive) will be called an *attractive (repulsive) closed limit curve* since its properties are similar to those of the limit cycles of a continuous dynamical system. By definition, a *limit cycle* is a simple closed curve which is the α– or the ω–limit set for at least one outside orbit (see e.g. Hirsch & Smale 1976). We shall avoid the term 'cycle' in the discrete time context since a cycle is usually associated with a periodic motion. Obviously, a countable orbit of a discrete dynamical system cannot fill a continuum. Accordingly, each limit curve consists of many orbits and in most cases none of them is a periodic one. Usually, the dynamical behaviour on a closed limit curve consists of a complicated pattern of quasi–periodic motions.

In many cases, closed limit curves encircling a fixed point arise from a *discrete Hopf bifurcation.* Such a bifurcation occurs within a one–parameter family (G_μ) of two–dimensional discrete dynamical systems whenever an associated family (p^*_μ) of fixed points loses its stability at a *critical parameter value* $\mu = \mu_0$ since a pair of complex conjugate eigenvalues cross the unit circle. This means that p^*_μ is a hyperbolic attractor for $\mu < \mu_0$ and a hyperbolic repellor for $\mu > \mu_0$ (a more exact definition of a Hopf bifurcation will be given below).

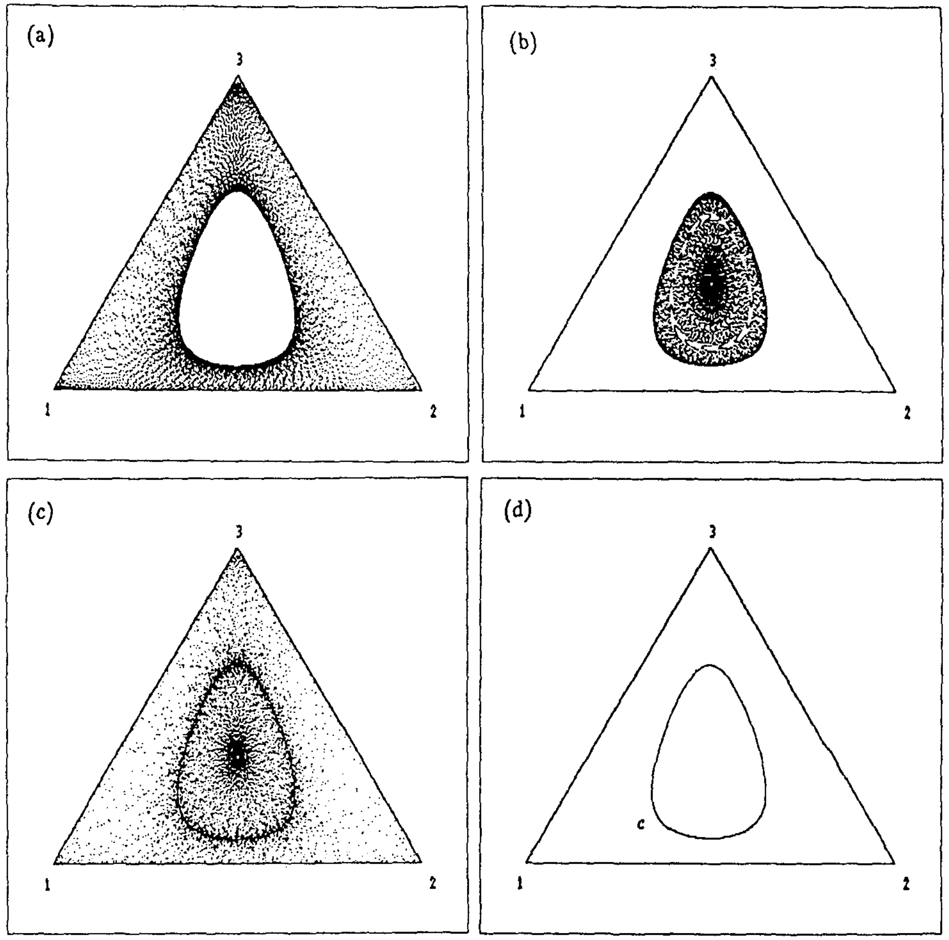


FIGURE 6: Existence of a closed limit curve for the discrete replicator dynamics. This figure shows some orbits of (6.1) for the central RSP–game

$$A = \begin{bmatrix} 10.00 & 11.50 & 9.00 \\ 9.00 & 10.00 & 11.50 \\ 15.85 & 4.65 & 10.00 \end{bmatrix}.$$

(a) Orbit starting at $p = (0.01, 0.01, 0.98)$ (iterated for 20,000 generations).

(b) Orbit starting at $p = (0.33, 0.33, 0.34)$ (36,000 generations; only every third generation is shown).

(c) Superimposition of the orbits in (a) and (b) (only every fifth generation is shown).

(d) Orbit starting at $p = (0.461, 0.461, 0.078)$ which closely approximates the closed limit curve $\mathcal{C}$.

In essence, there are three types of discrete Hopf bifurcations:

(a) *Subcritical* Hopf bifurcations.
For 'subcritical' parameter values, i.e., for parameter values μ which are slightly smaller than the critical value μ_0, the *stable* fixed point $\mathbf{p}^*_\mu$ is encircled by a repelling closed limit curve C_μ which circumscribes the domain of attraction of $\mathbf{p}^*_\mu$. The family (C_μ) of closed curves shrinks to the fixed point $\mathbf{p}^*_{\mu_0}$ (and the domains of attraction get smaller and smaller) if μ tends towards μ_0 from below.

(b) *Supercritical* Hopf bifurcations.
For 'supercritical' parameter values μ which are slightly larger than the critical value μ_0, the *unstable* fixed point $\mathbf{p}^*_\mu$ is encircled by an attracting closed limit curve C_μ which circumscribes the 'domain of repulsion' of $\mathbf{p}^*_\mu$. The family (C_μ) shrinks to the fixed point $\mathbf{p}^*_{\mu_0}$ if μ tends towards μ_0 from above.

(c) *Degenerate* Hopf bifurcations.
This is a class of Hopf bifurcations where closed limit curves do not arise. Instead, a picture like that obtained for circulant games (see Theorem 6.8) is rather typical: the center $\mathbf{p}^*_{\mu_0}$ is surrounded by a family of closed invariant curves, and no closed invariant curves exist near $\mathbf{p}^*_\mu$ for $\mu \neq \mu_0$.

Figure 7 indicates that the attracting closed limit curve of Figure 6 also results from a discrete supercritical Hopf bifurcation. It is the aim of this section to give an analytical proof for this assertion. In view of Theorem 6.3, it is easy to see when a discrete Hopf bifurcation does occur in the RSP–game context. In fact, the eigenvalues of the interior fixed point of an RSP–game with respect to the discrete replicator dynamics cross the unit circle of the complex plane whenever we have:

$$\det(A_0) > 0, \quad \sum_i \gamma_i\gamma_{i+1} > 0, \quad \text{and} \quad \mathbf{a}\cdot\mathbf{p}^* = \psi(A_0). \tag{7.1}$$

As in most other applications, it is not difficult to judge whether a discrete Hopf bifurcations occurs. However, it is usually quite intricate to classify a given Hopf bifurcation and to demonstrate that it is of the supercritical type.

The Hopf bifurcation illustrated by Figure 7 occurs in a one–parameter family of discrete replicator dynamics $(\mathcal{T}_\mu)_{\mu>0}$ arising from the family of central RSP–games which are given by

$$A_\mu = \begin{bmatrix} a & b & c \\ c & a & b \\ b+3\mu & c-3\mu & a \end{bmatrix}, \quad b > a \geq c, \quad c \geq 3\mu > 0. \tag{7.2}$$

Proposition 6.1 indicates that a discrete Hopf bifurcation occurs at the critical value

$$\mu_0 = \frac{bc-a^2}{b-c}. \tag{7.3}$$

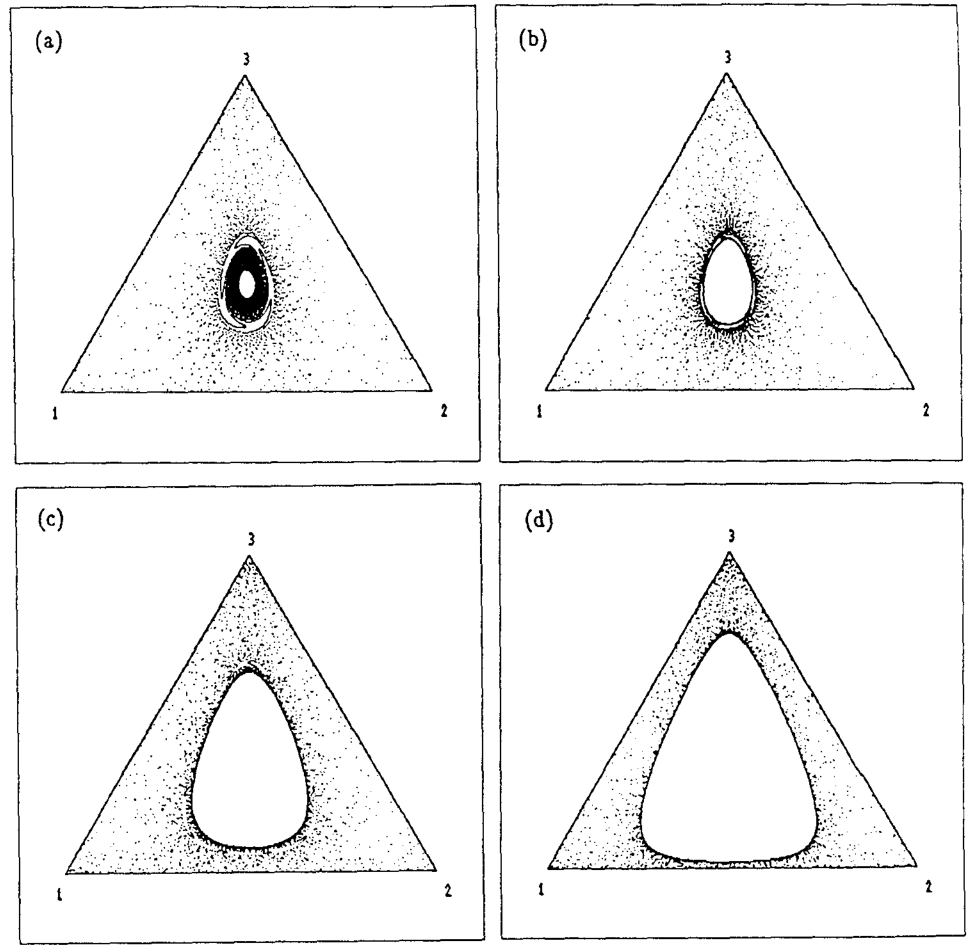


FIGURE 7: A discrete supercritical Hopf bifurcation (occuring at $\mu_0 = 1.40$) which is induced by the one–parameter family of central RSP–games given by:

$$A_\mu = \begin{bmatrix} a & b & c \\ c & a & b \\ b+3\mu & c-3\mu & a \end{bmatrix}, \text{ where } a = 10,\ b = 11.5,\ c = 9.$$

Orbit starting at $\mathbf{p} = (0.01, 0.01, 0.98)$ for:

(a) $\mu = 1.401$,
(b) $\mu = 1.41$,
(c) $\mu = 1.45$,
(d) $\mu = 1.50$.

(c) corresponds to the example in Figure 6. See text for details.

In fact, the interior fixed point $p^*_\mu = m$ of A_μ is a discrete hyperbolic attractor for $\mu < \mu_0$ while it is a hyperbolic repellor for $\mu > \mu_0$. For $\mu = \mu_0$, the eigenvalues of the linearization of $\mathcal{T}_\mu$ at p^*_μ are one in modulus, i.e., they belong to the unit circle in the complex plane.

The numerical example in Figure 7 suggests that the Hopf bifurcation at μ_0 is a supercritical one: For parameter values μ which are slightly larger than μ_0, an attracting closed limit curve arises, the 'radius' of which increases with increasing distance of μ to μ_0. We have seen that this phenonemon is typical for a supercritical Hopf bifurcation.

In the rest of this section, we shall complement the numerical results of Figures 6 and 7 by proving analytically that – at least for certain parameter constellations – the Hopf bifurcation described above is of the supercritical type. More precisely, we shall show:

<u>THEOREM 7.1:</u> Existence of supercritical discrete Hopf bifurcations.

Let $(\mathcal{T}_\mu)$ denote the one–parameter family of discrete replicator dynamics arising from the family (A_μ) of central RSP–games which are given by (7.2). Suppose that a is related to b and c via

$$a^2 = bc - \tfrac{1}{2}\cdot(b-c)^2, \tag{7.4}$$

and that

$$b < \tfrac{5}{3}\cdot c. \tag{7.5}$$

Then, the critical value μ_0 for $(\mathcal{T}_\mu)$ is given by

$$\mu_0 = \tfrac{1}{2}\cdot(b-c), \tag{7.6}$$

and the discrete Hopf bifurcation occuring at μ_0 is of the supercritical type.

The significance of conditions (7.4) and (7.5) will become clear from the proof of Theorem 7.1. (7.4) is not really needed, but the proof is simplified considerably if it holds true. (7.5) ensures that the matrix A_μ remains non–negative for all μ which are slightly larger than μ_0. Notice that the set of parameter constellations (a,b,c) satisfying (7.4) and (7.5) is not empty. For example, the triple (13,17,11) satisfies (7.4) and (7.5) as well as the inequalities in (7.2).

Let us state the main conclusion of Theorem 7.1 as a corollary:

<u>COROLLARY 7.2:</u> Existence of attracting closed limit curves.

There are discrete replicator dynamics which are induced by RSP–games and which admit an attracting closed limit curve.

To my knowledge, this is the first time that closed limit curves are described for the discrete replicator dynamics. There is, however, an 'indirect' proof of their existence in higher dimensions. Hofbauer & Iooss (1984) have shown that a supercritical Hopf bifurcation for the continuous replicator dynamics induces a bifurcation of the same type for the discrete replicator equation if selection is 'weak' enough. This result is not applicable here, since supercritical Hopf bifurcations do not occur for the continuous replicator dynamics if only three pure strategies are involved like in our RSP–games (see Hofbauer 1981).

Before we come to the proof of Theorem 7.1, we shall cite some general results on discrete Hopf bifurcations from dynamical systems theory (see e.g. Guckenheimer & Holmes 1983, Chapter 3.5). Consider a one–parameter family of two–dimensional discrete dynamical systems G_μ that has a smooth family of fixed points p^*_μ at which the eigenvalues of the linearization $DG_\mu(p^*_\mu)$ are complex conjugate to another. Suppose that $\lambda(\mu)$ denotes one of the two eigenvalues of $DG_\mu(p^*_\mu)$ and that $\lambda(\mu)$ is a smooth function of μ. A *discrete Hopf bifurcation* occurs at the parameter $\mu = \mu_0$, if the family of eigenvalues $\lambda(\mu)$ crosses the unit circle of the complex plane at μ_0 with a positive velocity, i.e., if the following two conditions hold true:

$$|\lambda(\mu_0)| = 1, \tag{7.7}$$

$$\frac{d}{d\mu}(|\lambda(\mu)|)_{\mu=\mu_0} = v > 0. \tag{7.8}$$

(7.7) and (7.8) imply that (for μ near the bifurcation point μ_0) the fixed point p^*_μ is hyperbolically stable for $\mu < \mu_0$ and hyperbolically unstable for $\mu > \mu_0$. Bifurcation structures associated with eigenvalues $\lambda(\mu_0)$ which are third or fourth roots of unity have some special features (see Iooss 1979). Let us neglect these *resonance cases* and assume that

$$\lambda^j(\mu_0) \neq 1 \text{ for } j = 1, 2, 3, 4, \tag{7.9}$$

or equivalently

$$\lambda(\mu_0) \notin \mathbb{R},\ \lambda(\mu_0) \notin i\cdot\mathbb{R} \text{ and } \mathrm{Re}(\lambda(\mu_0)) \neq -\tfrac{1}{2}. \tag{7.10}$$

A famous theorem from the theory of dynamical systems (see Marsden & McCracken 1976, Iooss 1979, Guckenheimer & Holmes 1983) states that under the conditions (7.7), (7.8), and (7.9) there is a smooth change of coordinates H so that the expression of $H \circ G_\mu \circ H^{-1}$ in polar coordinates has the form:

$$H \circ G_\mu \circ H^{-1}(r,\theta) = (r(1+v(\mu-\mu_0)-wr^2),\ \theta+s+tr^2) + \Omega(r,\theta), \tag{7.11}$$

where

$$s := |\arg(\lambda(\mu_0))| \neq 0 \tag{7.12}$$

denotes the argument of $\lambda(\mu_0)$, whereas $\Omega(r,\theta)$ collects all higher–order terms.

Notice that the first component of (7.11) can be represented in the form

$$r' = r\cdot(1 + v(\mu-\mu_0) - wr^2) + \Omega_1(r,\theta). \tag{7.13}$$

Consequently, for $w \neq 0$ a third–order approximation may be written as

$$\frac{\Delta r}{wr} = \frac{v}{w}\cdot(\mu-\mu_0) - r^2. \tag{7.14}$$

Depending on the sign of w, the truncated dynamical system (7.14) has either for all $\mu < \mu_0$ or for all $\mu > \mu_0$ a fixed point $r^*_\mu > 0$ which is given by:

$$r^*_\mu = \sqrt{\frac{v}{w}\cdot(\mu-\mu_0)}, \quad \text{if} \quad \mathrm{sgn}(w) = \mathrm{sgn}(\mu-\mu_0) \neq 0. \tag{7.15}$$

For those μ for which $\mathrm{sgn}(w) = \mathrm{sgn}(\mu-\mu_0)$, (7.14) can be written in the form

$$\Delta r = rw\cdot(\,(r^*_\mu)^2 - r^2). \tag{7.14a}$$

(7.14a) shows that the stability of r^*_μ also depends on the sign of w: r^*_μ is an attractor *if* $w > 0$ and a repellor if $w < 0$. Obviously, r^*_μ is the radius of a circle which is invariant with respect to the third–order approximation of $\mathrm{H}\circ\mathrm{G}_\mu\circ\mathrm{H}^{-1}$, and the circle is an attractive (a repulsive) closed limit curve if and only if r^*_μ is an attractor (a repellor) of (7.14a).

These considerations show that the sign of the *Hopf parameter* w is of crucial importance for the dynamical behaviour of the bifurcating system: The Hopf bifurcation is supercritical if w is positive, and it is subcritical if w is negative. Nothing definite can be said if the Hopf parameter of the bifurcating system is equal to zero. In this case, higher order terms have to be considered. 'Generically', the bifurcation is again either supercritical or subcritical (see Iooss 1979). In applications, however, the condition $w = 0$ often implies that the Hopf bifurcation is a degenerate one (as in the case of circulant RSP–games).

We shall now present a formula (see (7.19)) which allows us to calculate the Hopf parameter of a bifurcating system by having a closer look at the higher order terms of the bifurcating map G_{μ_0} near the fixed point $\mathrm{p}^*_{\mu_0}$. This formula may be derived by transforming G_{μ_0} to 'normal form' (see Iooss 1979). A complex coordinate version of it was developed by Wan (1978). In slightly modified form, the real coordinate version given below may be found in Guckenheimer & Holmes (1983).

The calculation of the Hopf parameter w is simplified considerably, if the linear part of the bifurcating system $\mathrm{G}_{\mu_0}\colon \mathbb{R}^2 \longrightarrow \mathbb{R}^2$ at the fixed point $\mathrm{p}^*_{\mu_0}$ is in real Jordan form. Let us call the $\mathbb{R}^2$–coordinates *Jordan coordinates* if $\mathrm{DG}_{\mu_0}(\mathrm{p}^*_{\mu_0})$ is of the form

$$\mathrm{DG}_{\mu_0}(\mathrm{p}^*_{\mu_0}) = \begin{bmatrix} \mathrm{Re}(\lambda) & -\mathrm{Im}(\lambda) \\ \mathrm{Im}(\lambda) & \mathrm{Re}(\lambda) \end{bmatrix}, \quad \text{where } \lambda = \lambda(\mu_0). \tag{7.16}$$

Suppose that a Jordan coordinate representation of G_{μ_0} is given by

$$\mathrm{G}_{\mu_0}(x,y) = \begin{bmatrix} \mathrm{f}(x,y) \\ \mathrm{g}(x,y) \end{bmatrix}, \tag{7.17}$$

where f and g are scalar functions. Let us for the rest of this section use the convention that terms like $\mathrm{f_i}$, $\mathrm{g_{ij}}$, or $\mathrm{h_{ijj}}$ denote (higher order) partial derivatives of f, g, and h with respect to the i'th and j'th coordinate which are evaluated at the fixed point $\mathrm{p}^*_{\mu_0}$, e.g.:

$$\mathrm{f}_{12} := \frac{\partial^2}{\partial x \partial y}\mathrm{f}(\mathrm{p}^*_{\mu_0}), \quad \text{or} \quad \mathrm{g}_{22} := \frac{\partial^2}{\partial y^2}\mathrm{g}(\mathrm{p}^*_{\mu_0}). \tag{7.18}$$

Now the Hopf parameter w can be obtained from the formula (Guckenheimer & Holmes 1983, p.163):

$$w = \frac{1}{16}\cdot\Big[\, \mathrm{Re}(\xi_0\xi_A\xi_B) + \tfrac{1}{2}\cdot|\xi_B|^2 + |\xi_C|^2 - \mathrm{Re}(\overline{\lambda}\xi_D) \,\Big], \tag{7.19}$$

where ξ_0, ξ_A, ξ_B, ξ_C, and ξ_D are given by:

$$\xi_0 = \frac{(1-2\lambda)\overline{\lambda}^2}{1-\lambda}, \tag{7.20}$$

$$\xi_A = \tfrac{1}{2}\cdot((\mathrm{f}_{11} - \mathrm{f}_{22} + 2\mathrm{g}_{12}) + i\cdot(\mathrm{g}_{11} - \mathrm{g}_{22} - 2\mathrm{f}_{12})), \tag{7.21}$$

$$\xi_B = (\mathrm{f}_{11} + \mathrm{f}_{22}) + i\cdot(\mathrm{g}_{11} + \mathrm{g}_{22}), \tag{7.22}$$

$$\xi_C = \tfrac{1}{2}\cdot((\mathrm{f}_{11} - \mathrm{f}_{22} - 2\mathrm{g}_{12}) + i\cdot(\mathrm{g}_{11} - \mathrm{g}_{22} + 2\mathrm{f}_{12})), \tag{7.23}$$

$$\xi_D = (\mathrm{f}_{111} + \mathrm{f}_{122} + \mathrm{g}_{112} + \mathrm{g}_{222}) + i\cdot(\mathrm{g}_{111} + \mathrm{g}_{122} - \mathrm{f}_{112} - \mathrm{f}_{222}). \tag{7.24}$$

Notice that $\lambda := \lambda(\mu_0)$ and therefore $|\lambda| = 1$, i.e.,

$$\lambda\cdot\overline{\lambda} = (\mathrm{Re}(\lambda))^2 + (\mathrm{Im}(\lambda))^2 = 1. \tag{7.25}$$

It is easy to see that this implies

$$|1-\lambda|^2 = 2\cdot(1-\mathrm{Re}(\lambda)), \tag{7.26}$$

and

$$\frac{1-2\lambda}{1-\lambda} = 1 + \frac{1-\overline{\lambda}}{|1-\lambda|^2} = \frac{3}{2} - \frac{\mathrm{Im}(\lambda)}{2(1-\mathrm{Re}(\lambda))}\cdot i. \tag{7.27}$$

On the other hand, (7.25) yields

$$\mathrm{Re}(\overline{\lambda}^2) = 2\cdot(\mathrm{Re}(\lambda))^2 - 1, \tag{7.28}$$

$$\mathrm{Im}(\overline{\lambda}^2) = 2\cdot\mathrm{Re}(\lambda)\cdot\mathrm{Im}(\lambda). \tag{7.29}$$

Applying (7.27), (7.28), and (7.29), it is easy to see that the parameter ξ_0 is of the form:

$$\mathrm{Re}(\xi_0) = \mathrm{Re}(\lambda)\cdot(2\cdot\mathrm{Re}(\lambda)-1) - \tfrac{3}{2}, \tag{7.30}$$

$$\mathrm{Im}(\xi_0) = -\mathrm{Im}(\lambda)\cdot(2\cdot\mathrm{Re}(\lambda)-1) - \frac{\mathrm{Im}(\lambda)}{2(1-\mathrm{Re}(\lambda))}. \tag{7.31}$$

In order to calculate the other parameters ξ_A, ξ_B, ξ_C, and ξ_D, we have to know some of the higher order derivatives of the functions f and g.

If we want to apply (7.19) to a Hopf bifurcation arising in the context of the discrete replicator dynamics, we have to proceed as follows: First, the bifurcating replicator equation has to be transformed to a discrete dynamical system on $\mathbb{R}^2$. Then, we have to calculate the linearization at the interior fixed point. Transforming the linearization into real Jordan form gives us Jordan coordinates and the representation (7.17). On the basis of f and g, we may then calculate the ξ's and the Hopf parameter w.

Let $(\mathcal{I}_\mu)$ denote any one–parameter family of discrete replicator equations $\mathbf{p}' = \mathcal{I}_\mu(\mathbf{p})$ which is induced by a one–parameter family of central evolutionary 3x3 normal form games (A_μ). Then $\mathcal{I}_\mu: \Delta \longrightarrow \Delta$ is a mapping which is given by

$$(\mathcal{I}_\mu(\mathbf{p}))_i = \frac{p_i\cdot(A_\mu \mathbf{p})_i}{\mathbf{p}\cdot A_\mu \mathbf{p}}, \quad \mathbf{p}\in\Delta,\ i\in I. \tag{7.32}$$

Each mapping $\mathcal{I}_\mu$ has an interior fixed point in the barycenter $\mathbf{m}$ of the strategy simplex. Setting $\mathbf{p} = \mathbf{m} + \mathbf{z}$, $\mathbf{z}\in\mathbb{R}^3_0$, we get $\mathbf{z}' = \mathbf{p}' - \mathbf{m} = \mathcal{I}_\mu(\mathbf{m}+\mathbf{z}) - \mathbf{m}$. Accordingly, the discrete dynamical system $\mathcal{I}_\mu$ on Δ can be transformed to an equivalent system $\mathcal{S}_\mu$ on a subset $\Delta_\mathcal{S}$ of $\mathbb{R}^3_0$, where $\Delta_\mathcal{S}$ and $\mathcal{S}_\mu: \Delta_\mathcal{S} \longrightarrow \Delta_\mathcal{S}$ are defined by

$$\Delta_\mathcal{S} := \{\, \mathbf{z}\in\mathbb{R}^3_0 \mid \mathbf{m}+\mathbf{z}\in\Delta \,\}, \tag{7.33}$$

$$\mathcal{S}_\mu(\mathbf{z}) := \mathcal{I}_\mu(\mathbf{m}+\mathbf{z}) - \mathbf{m}, \quad \mathbf{z}\in\Delta_\mathcal{S}. \tag{7.34}$$

Each mapping $\mathcal{S}_\mu$ has a unique interior fixed point in the zero vector 0. If we identify $\mathbb{R}^3_0$ with $\mathbb{R}^2$ by means of the canonical isomorphism $\mathrm{P}: \mathbb{R}^3_0 \longrightarrow \mathbb{R}^2$ (see (4.10)), we get an equivalent representation $\mathcal{G}_\mu$ of $\mathcal{I}_\mu$ on a subset $\Delta_\mathcal{G}$ of $\mathbb{R}^2$. Obviously, $\Delta_\mathcal{G}$ and $\mathcal{G}_\mu: \Delta_\mathcal{G} \longrightarrow \Delta_\mathcal{G}$ are given by

$$\Delta_\mathcal{G} := \mathrm{P}(\Delta_\mathcal{S}), \quad \mathcal{G}_\mu := \mathrm{P}^{-1}\circ\mathcal{S}_\mu\circ\mathrm{P}. \tag{7.35}$$

In essence, $\mathcal{G}_\mu(z_1,z_2)$ results from $\mathcal{S}_\mu(z_1,z_2,z_3)$ by replacing z_3 by $-z_1-z_2$ and by discarding the third component of the vector $\mathcal{S}_\mu(\mathbf{z})$.

The linearization of $\mathcal{G}_{\mu_0}$ at its unique interior fixed point 0 (which corresponds to $\mathbf{p}^* = \mathbf{m}$) is given by (6.6), (6.5), and (5.25). Let us suppose that the linearization of $\mathcal{G}_{\mu_0}$ is in real Jordan form and that f and g denote the components of $\mathcal{G}_{\mu_0}$ with respect to these Jordan coordinates:

$$\mathcal{G}_{\mu_0}(x,y) = (\, \mathrm{f}(x,y),\ \mathrm{g}(x,y) \,). \tag{7.36}$$

It is easy to see that the scalar functions f and g are of the form

$$\mathrm{f}(x,y) = \frac{\mathrm{n}^\mathrm{f}(x,y)}{\mathrm{d}(x,y)} - \frac{1}{3}, \tag{7.37}$$

$$\mathrm{g}(x,y) = \frac{\mathrm{n}^\mathrm{g}(x,y)}{\mathrm{d}(x,y)} - \frac{1}{3}, \tag{7.38}$$

where the common denominator $\mathrm{d}(x,y)$ corresponds to mean fitness. In particular, we have

$$C := \mathrm{d}(0) = \mathcal{F}(\mathbf{m}). \tag{7.39}$$

Notice that

$$\mathrm{f}(0) = \mathrm{g}(0) = 0, \tag{7.40}$$

since 0 is a fixed point of $\mathcal{G}_{\mu_0}$. In order to get the Hopf parameter w, we have to evaluate some higher order partial derivatives of f and g at the interior fixed point 0. Since f and g are rational functions, the expressions for these partial derivatives are quite cumbersome. We shall circumvent this problem by deriving some recursive formulae for the terms f_{ij}, g_{ij}, f_{iij}, and g_{iij} which make it superfluous to calculate the partial derivatives of f and g explicitly.

It is easy to see that the numerators and the denominator of f and g are polynomials of degree two, the derivatives of which are easy to calculate. In particular, all those partial derivatives of n^f, n^g, and d vanish which are of third and higher order. Using this fact together with (7.39) and (7.40), the quotient rule of differentiation yields the following formulae for the partial derivatives of f evaluated at the origin:

$$\mathrm{f}_i = \tfrac{1}{C}\cdot(\, \mathrm{n}^\mathrm{f}_i - \tfrac{1}{3}\cdot\mathrm{d}_i \,), \tag{7.41}$$

$$\mathrm{f}_{ij} = \tfrac{1}{C}\cdot(\, \mathrm{n}^\mathrm{f}_{ij} - \tfrac{1}{3}\cdot\mathrm{d}_{ij} - \mathrm{f}_i\mathrm{d}_j - \mathrm{f}_j\mathrm{d}_i \,), \tag{7.42}$$

$$\mathrm{f}_{iij} = \tfrac{1}{C}\cdot(\, -\mathrm{f}_j\mathrm{d}_{ii} - 2\mathrm{f}_i\mathrm{d}_{ij} - 2\mathrm{f}_{ij}\mathrm{d}_i - \mathrm{f}_{ii}\mathrm{d}_j \,). \tag{7.43}$$

Of course, the corresponding expressions for g_i, g_{ij}, and g_{iij} are completely analogous. Notice that by definition the linarization J_{μ_0} of $\mathcal{G}_{\mu_0}$ at 0 is of the form

$$J_{\mu_0} = \begin{bmatrix} \mathrm{f}_1 & \mathrm{f}_2 \\ \mathrm{g}_1 & \mathrm{g}_2 \end{bmatrix}. \tag{7.44}$$

If we are dealing with Jordan coordinates, a comparison of (7.44) and (7.16) yields

$$f_1 = \mathrm{Re}(\lambda), \quad f_2 = -\mathrm{Im}(\lambda), \tag{7.45}$$

$$g_1 = \mathrm{Im}(\lambda), \quad g_2 = \mathrm{Re}(\lambda). \tag{7.46}$$

We shall see later that the calculation of ξ_A, ξ_B, and ξ_C is simplified considerably if these expressions are inserted into (7.42).

All these preparatory remarks hold true for *any* Hopf bifurcation arising in a one–parameter family of discrete replicator equations. We have presented them in some generality in order to indicate how the techniques for calculating the Hopf parameter w can be applied to 3x3 normal form games which go beyond the class of RSP–games. Let us now apply these considerations to the class of RSP–games which is given by (7.2).

PROOF OF THEOREM 7.1:

A: Let from now on denote $(\mathcal{T}_\mu)_{\mu>0}$ the one–parameter family of discrete replicator dynamics which is induced by the family (A_μ) of central RSP–games given by (7.2). Let $(\mathcal{G}_\mu)$ be the corresponding family of mappings which is defined by (7.35). With respect to canonical $\mathbb{R}^2$–coordinates, *the linearization* $D\mathcal{G}_\mu(0)$ *of* $\mathcal{G}_\mu$ *at its unique interior fixed point* 0 *is* characterized by a matrix J_μ which is defined by (6.6), (6.5), and (5.25). Let $\lambda(\mu)$ denote one of the two complex conjugate eigenvalues of J_μ and suppose that $\lambda(\mu)$ is chosen in a way that makes it smoothly dependent on the parameter μ.

From the results of Section 6 we know already that the parameter μ_0 which is defined by (7.3) is a candidate for being the critical value for a discrete Hopfbifurcation, since

$$|\lambda(\mu)| \begin{cases} <1 & \text{for } \mu < \mu_0 \\ =1 & \text{for } \mu = \mu_0 \, . \\ >1 & \text{for } \mu > \mu_0 \end{cases} \tag{7.47}$$

Of course, it is necessary that A_{μ_0} is an admissible (i.e., a non–negative) payoff matrix for the discrete replicator dynamics. For this to be true, we need $c \geq 3\mu_0$, and we shall even require $c > 3\mu_0$ since we are also interested in μ's which are slightly larger than μ_0. It is easy to see that $c > 3\mu_0$ *is equivalent to:*

$$bc > a^2 > bc - \tfrac{1}{3}\, c(b-c). \tag{7.48}$$

Together with (6.6) and (6.5), (5.28) implies that the matrix J_μ is given by

$$J_\mu = \frac{1}{3\cdot C}\begin{bmatrix} 2a+b-\mu & b-c+\mu \\ -b+c-\mu & 2a+c+\mu \end{bmatrix}, \tag{7.49}$$

where C denotes the mean fitness at the interior fixed point $\mathbf{p}^* = \mathbf{m}$:

$$C := \mathcal{F}(\mathbf{m}) = \tfrac{1}{3}\cdot(a+b+c). \tag{7.50}$$

We have already shown that the eigenvalues $\lambda(\mu)$ and $\overline{\lambda}(\mu)$ of J_μ are complex conjugate to another. Consequently, the modulus of $\lambda(\mu)$ corresponds to the square root of the determinant of J_μ, and (7.8) is equivalent to:

$$\frac{d}{d\mu}\,(\det(J_\mu))_{\mu=\mu_0} > 0. \tag{7.51}$$

In view of

$$\frac{d}{d\mu}\,(\det(J_\mu)) = \frac{b-c}{C} > 0\,, \tag{7.52}$$

all criteria for the occurrence of a discrete Hopf bifurcation at μ_0 are fulfilled.

B: Inspection of (7.49) shows that J_{μ_0} is already in real Jordan form if its diagonal elements are equal to another, i.e., if

$$2a + b - \mu_0 = 2a + c + \mu_0, \tag{7.53}$$

or equivalently

$$\mu_0 = \tfrac{1}{2}\cdot(b-c). \tag{7.54}$$

Accordingly, we are already dealing with Jordan coordinates if (7.3) and (7.53) are satisfied simultaneously, i.e., if a, b, and c are related to another according to:

$$a^2 = bc - \tfrac{1}{2}\cdot(b-c)^2. \tag{7.55}$$

If (7.55) holds, (7.48) is equivalent to

$$c > \tfrac{3}{5}\cdot b. \tag{7.56}$$

Notice that (7.56) corresponds to (7.5), and that (7.55) is identical to (7.4). Accordingly, assumption (7.4) allows us to circumvent the awkward procedure of transforming $\mathcal{G}_{\mu_0}$ to Jordan coordinates, whereas (7.5) guarantees that A_μ is an admissible payoff matrix for the discrete replicator dynamics for all μ which are slightly larger than μ_0. Let us from now on suppose that these two conditions aresatisfied.

C: A comparison of (7.49) with (7.16) shows that the eigenvalue $\lambda(\mu_0)$ at the critical value μ_0 is given by

$$\lambda := \lambda(\mu_0) = \frac{1}{2\cdot C}(\,(a+C) - i\cdot(b-c)\,). \tag{7.57}$$

(It is important to take that eigenvalue of J_{μ_0} which has a negative imaginary part, since otherwise (7.16) and (7.49) would not correspond to another.)

It is obvious from (7.57) that λ is neither real nor purely imaginary. On the other hand, (7.56) together with $c \leq a$ implies $a+c > b$. It is easy to see that this inequality yields

$$|\mathrm{Im}(\lambda)| < |\mathrm{Re}(\lambda)|. \tag{7.58}$$

(7.58) implies that (7.10) holds true, i.e., that λ is neither a third nor a fourth root of unity: the Hopf bifurcation is non–resonant if (7.4) and (7.5) are satisfied.

D: Let us now consider the coordinate representation (7.36) of $\mathcal{G}_{\mu_0}$. Since the canonical $\mathbb{R}^2$–coordinates are already Jordan coordinates, it is easy to calculate the scalar functions f and g. In view of (7.37) and (7.38), they are determined by:

$$\mathrm{n}^{\mathrm{f}}(x,y) := \tfrac{1}{3}\cdot C + \tfrac{1}{3}(2a+b)x + \tfrac{1}{3}(b-c)y + (a-c)x^2 + (b-c)xy, \tag{7.59}$$

$$\mathrm{n}^{\mathrm{g}}(x,y) := \tfrac{1}{3}\cdot C - \tfrac{1}{3}(b-c)x + \tfrac{1}{3}(2a+c)y - (b-a)y^2 - (b-c)xy, \tag{7.60}$$

$$\mathrm{d}(x,y) := C - (b+c-2a)(x^2+y^2+xy) - \mu_0\cdot(3x^2-3y^2-x+y). \tag{7.61}$$

Notice that (7.61) yields

$$\mathrm{d}_1 = -\,\mathrm{d}_2 = \mu_0 = \tfrac{1}{2}\cdot(b-c). \tag{7.62}$$

E: On the basis of (7.42), we shall now calculate the terms f_{ij} and g_{ij}. In order to do this, let us introduce the notation

$$\mathrm{N}^{\mathrm{f}}_{ij} := \mathrm{n}^{\mathrm{f}}_{ij} - \tfrac{1}{3}\cdot\mathrm{d}_{ij}, \quad \mathrm{N}^{\mathrm{g}}_{ij} := \mathrm{n}^{\mathrm{g}}_{ij} - \tfrac{1}{3}\cdot\mathrm{d}_{ij}. \tag{7.63}$$

Now, (7.42) together with (7.45), (7.46), and (7.62) leads to the expressions

$$\mathrm{f}_{11} = \frac{1}{C}\cdot(\ \mathrm{N}^{\mathrm{f}}_{11} - 2\cdot\mu_0\cdot\mathrm{Re}(\lambda)\ ), \tag{7.64}$$

$$\mathrm{f}_{12} = \frac{1}{C}\cdot(\ \mathrm{N}^{\mathrm{f}}_{12} + \mu_0\cdot(\mathrm{Re}(\lambda)+\mathrm{Im}(\lambda))\ ), \tag{7.65}$$

$$\mathrm{f}_{22} = \frac{1}{C}\cdot(\ \mathrm{N}^{\mathrm{f}}_{22} - 2\cdot\mu_0\cdot\mathrm{Im}(\lambda)\ ), \tag{7.66}$$

$$\mathrm{g}_{11} = \frac{1}{C}\cdot(\ \mathrm{N}^{\mathrm{g}}_{11} - 2\cdot\mu_0\cdot\mathrm{Im}(\lambda)\ ), \tag{7.67}$$

$$\mathrm{g}_{12} = \frac{1}{C}\cdot(\ \mathrm{N}^{\mathrm{g}}_{12} - \mu_0\cdot(\mathrm{Re}(\lambda)-\mathrm{Im}(\lambda))\ ), \tag{7.68}$$

$$\mathrm{g}_{22} = \frac{1}{C}\cdot(\ \mathrm{N}^{\mathrm{g}}_{22} + 2\cdot\mu_0\cdot\mathrm{Re}(\lambda)\ ). \tag{7.69}$$

It is easy to calculate the terms $\mathrm{N}^{\mathrm{f}}_{ij}$ and $\mathrm{N}^{\mathrm{g}}_{ij}$. In view of (7.59), (7.60), and (7.61), we get

$$\mathrm{N}^{\mathrm{f}}_{11} = \tfrac{1}{3}\cdot(2a + 5b - 7c), \tag{7.70}$$

$$\mathrm{N}^{\mathrm{f}}_{12} = -\tfrac{2}{3}\cdot(a - 2b + c), \tag{7.71}$$

$$\mathrm{N}^{\mathrm{f}}_{22} = \tfrac{1}{3}\cdot(-4a - b + 5c), \tag{7.72}$$

$$\mathrm{N}^{\mathrm{g}}_{11} = \tfrac{1}{3}\cdot(-4a + 5b - c), \tag{7.73}$$

$$\mathrm{N}^{\mathrm{g}}_{12} = -\tfrac{2}{3}\cdot(a + b - 2c), \tag{7.74}$$

$$\mathrm{N}^{\mathrm{g}}_{22} = \tfrac{1}{3}\cdot(2a - 7b + 5c). \tag{7.75}$$

F: We shall now calculate the terms ξ_A, ξ_B, and ξ_C by inserting (7.64) to (7.69) into (7.21) to (7.23). The resulting formulae will be simplified by considering

$$\mathrm{Im}(\lambda) = -\,\mu_0/C \tag{7.76}$$

and the following identities:

$$\mathrm{N}^{\mathrm{f}}_{11} + \mathrm{N}^{\mathrm{f}}_{22} = \mathrm{N}^{\mathrm{f}}_{12}, \tag{7.77}$$

$$\mathrm{N}^{\mathrm{g}}_{11} + \mathrm{N}^{\mathrm{g}}_{22} = \mathrm{N}^{\mathrm{g}}_{12}, \tag{7.78}$$

$$\mathrm{N}^{\mathrm{f}}_{11} - \mathrm{N}^{\mathrm{f}}_{22} = -3\cdot\mathrm{N}^{\mathrm{g}}_{12}, \tag{7.79}$$

$$\mathrm{N}^{\mathrm{g}}_{11} - \mathrm{N}^{\mathrm{g}}_{22} = 3\cdot\mathrm{N}^{\mathrm{f}}_{12}. \tag{7.80}$$

ξ_A, ξ_B, and ξ_C are given by:

$$\mathrm{Re}(\xi_A) = -\frac{1}{2\cdot C}\cdot\mathrm{N}^{\mathrm{g}}_{12} + 2\cdot\mathrm{Im}(\lambda)\cdot(\mathrm{Re}(\lambda)-\mathrm{Im}(\lambda)), \tag{7.81}$$

$$\mathrm{Im}(\xi_A) = \frac{1}{2\cdot C}\cdot\mathrm{N}^{\mathrm{f}}_{12} + 2\cdot\mathrm{Im}(\lambda)\cdot(\mathrm{Re}(\lambda)+\mathrm{Im}(\lambda)), \tag{7.82}$$

$$\mathrm{Re}(\xi_B) = \frac{1}{C}\cdot\mathrm{N}^{\mathrm{f}}_{12} + 2\cdot\mathrm{Im}(\lambda)\cdot(\mathrm{Re}(\lambda)+\mathrm{Im}(\lambda)), \tag{7.83}$$

$$\mathrm{Im}(\xi_B) = \frac{1}{C}\cdot\mathrm{N}^{\mathrm{g}}_{12} - 2\cdot\mathrm{Im}(\lambda)\cdot(\mathrm{Re}(\lambda)-\mathrm{Im}(\lambda)), \tag{7.84}$$

$$\mathrm{Re}(\xi_C) = -\frac{5}{2\cdot C}\cdot 2\mathrm{N}^{\mathrm{g}}_{12}, \tag{7.85}$$

$$\mathrm{Im}(\xi_C) = \frac{5}{2\cdot C}\cdot 2\mathrm{N}^{\mathrm{f}}_{12}. \tag{7.86}$$

G: Inserting (7.71) and (7.74) into (7.83) to (7.86), we get in view of (7.25):

$$|\xi_C|^2 = \frac{25}{9C^2}\cdot\Big[\ (b-a)^2+(a-c)^2+4(b-c)^2\ \Big], \tag{7.87}$$

$$\tfrac{1}{2}\cdot|\xi_B|^2 = \frac{2}{25}\cdot|\xi_C|^2 + 4\cdot(\mathrm{Im}(\lambda))^2\cdot\Big[\ \frac{C\ -\ 2a}{C}\ \Big]. \tag{7.88}$$

Replacing $\mathrm{Im}(\lambda)$ by (7.76), this implies

$$\tfrac{1}{2}\cdot|\xi_B|^2+|\xi_C|^2 = \frac{1}{C^2}\cdot\Big[3(b-a)^2+3(a-c)^2+(\frac{13C-2a}{C})\cdot(b-c)^2\Big]. \tag{7.89}$$

Finally, notice that $\mathrm{Re}(\xi_0\xi_A\xi_B)$ is given by

$$\begin{aligned}\mathrm{Re}(\xi_0\xi_A\xi_B) = {} & \mathrm{Re}(\xi_0)\mathrm{Re}(\xi_A)\mathrm{Re}(\xi_B) - \mathrm{Re}(\xi_0)\mathrm{Im}(\xi_A)\mathrm{Im}(\xi_B) \\ & - \mathrm{Im}(\xi_0)\mathrm{Re}(\xi_A)\mathrm{Im}(\xi_B) - \mathrm{Im}(\xi_0)\mathrm{Im}(\xi_A)\mathrm{Re}(\xi_B).\end{aligned} \tag{7.90}$$

In view of (7.19), the only thing that is missing for the calculation of the Hopf parameter w is an expression for the parameter ξ_D. This will be derived next.

H: Using (7.43) together with (7.45), (7.46), and (7.62), we get the following formula for ξ_D:

$$\mathrm{Re}(\xi_D) = -\frac{1}{C}\cdot(\ \sigma'\cdot\mu_0 + 4\cdot\mathrm{Re}(\lambda)\cdot(d_{11}+d_{22})\ ), \tag{7.91}$$

$$\mathrm{Im}(\xi_D) = -\frac{1}{C}\cdot(\ \tau'\cdot\mu_0 + 4\cdot\mathrm{Im}(\lambda)\cdot(d_{11}+d_{22})\ ), \tag{7.92}$$

where σ' and τ' are defined by

$$\sigma' := 3(f_{11}-g_{22}) - 2(f_{12}-g_{12}) + (f_{22}-g_{11}), \tag{7.93}$$

$$\tau' := 3(f_{22}+g_{11}) - 2(f_{12}+g_{12}) + (f_{11}+g_{22}). \tag{7.94}$$

Inserting (7.64) to (7.69) into (7.93) and (7.94) and considering (7.76), we get the following simplified expressions for $\mathrm{Re}(\xi_D)$ and $\mathrm{Im}(\xi_D)$:

$$\mathrm{Re}(\xi_D) = \rho\cdot\mathrm{Re}(\lambda) + \sigma\cdot\mathrm{Im}(\lambda), \tag{7.95}$$

$$\mathrm{Im}(\xi_D) = (\rho+\tau)\cdot\mathrm{Im}(\lambda), \tag{7.96}$$

where ρ, σ, and τ are given by

$$\rho := 16\cdot(\mathrm{Im}(\lambda))^2 - 4\cdot\frac{d_{11}+d_{22}}{C}, \tag{7.97}$$

$$\sigma := \frac{1}{C}\cdot\left[3(N^f_{11}-N^g_{22}) - 2(N^f_{12}-N^g_{12}) + (N^f_{22}-N^g_{11})\right], \tag{7.98}$$

$$\tau := \frac{1}{C}\cdot\left[3(N^f_{22}+N^g_{11}) - 2(N^f_{12}+N^g_{12}) + (N^f_{11}+N^g_{22})\right]. \tag{7.99}$$

From (7.95) and (7.96), we get

$$\mathrm{Re}(\overline{\lambda}\cdot\xi_D) = \rho + \mathrm{Im}(\lambda)\cdot(\sigma\cdot\mathrm{Re}(\lambda) + \tau\cdot\mathrm{Im}(\lambda)). \tag{7.100}$$

I: We are now in the position to calculate the Hopf parameter w by inserting (7.89), (7.90), and (7.100) into (7.19). For example, we get $w = 0.012$ for the parameter constellation $(a,b,c) = (13,17,11)$.
The proof of Theorem 7.1 will be completed by showing that w is positive for *all* parameter constellations satisfying (7.4) and (7.5). Without loss in generality, we may assume $c = 1$, since the discrete replicator dynamics is not affected if the payoff matrix is multiplied by the

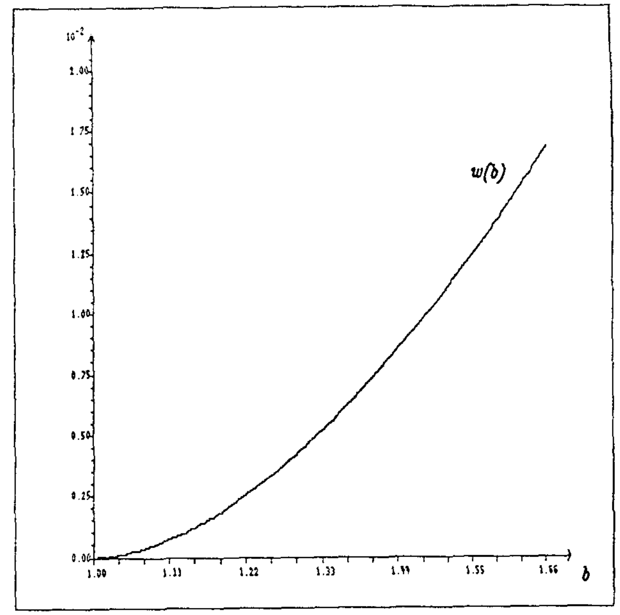


FIGURE 8: With c normalized to one, the Hopf parameter w is depicted as a function of b ($1 < b < 5/3$). For all admissible b, the Hopf parameter is positive, i.e., the Hopf bifurcation is a supercritical one.

positive scalar $1/c$. For any b which is compatible with (7.5) (i.e., $1 < b < 5/3$), the parameter a is fully specified by (7.4). Accordingly, the paramter w may be interpreted as a function of b. In Figure 8, w is depicted as a function of b. Obviously, we have $w(b) > 0$ for all b with $1 < b < 1.667$. This completes the proof.

* * *

From Figures 6 and 7, one might get the impression that the attracting closed limit curve arising from a discrete Hopf bifurcation as described above is a *global* attractor in the sense that it attracts all interior non–equilibrium orbits. Figure 9 shows that this impression is not necessarily correct.

The example in Figure 9 is based on a central RSP–game of the form (7.2) where (a,b,c) is given by (13,17,11). A discrete supercritical Hopf bifurcation occurs at the critical value $\mu_0 = 3$. For admissible parameter values μ which are slightly larger than 3 (Figure 9 shows the case $\mu = 3.25$), an attracting closed orbit C arises which attracts all nearby orbits including all those orbits starting in the region which is enclosed by C. However, C is not a global attractor. Instead, it is encircled by *another* invariant closed curve C' which is a repulsive limit curve for the discrete replicator dynamics. Figure 9 indicates that there are *two* attractors (the limit curve C and the boundary of the strategy simplex) whose domain of attraction is separated by C'.

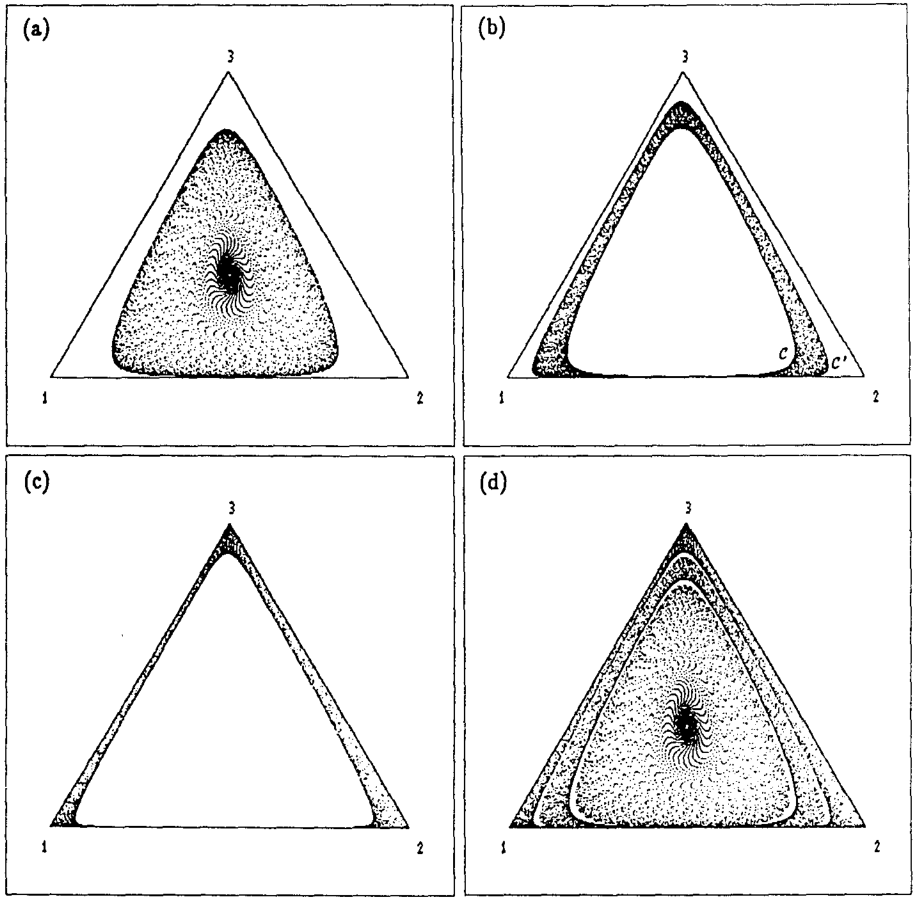


FIGURE 9: A discrete replicator dynamics with two attractors.
This figure shows some orbits of (6.1) for the central RSP–game

$$A = \begin{bmatrix} 13.00 & 17.00 & 11.00 \\ 11.00 & 13.00 & 17.00 \\ 26.75 & 1.25 & 13.00 \end{bmatrix}.$$

(a) Orbit starting at $p = (0.33,0.33,0.34)$. It converges to the attracting closed limit curve C.

(b) Orbit starting at $p = (0.05,0.05,0.90)$. It is repelled by C' and it converges to the limit curve C.

(c) Orbit starting at $p = (0.049,0.049,0.902)$. It is also repelled by C' and it converges to the boundary of the strategy simplex.

(d) Superposition of the three orbits.

8. Are RSP–Games Played in Biological Populations?

In the previous sections, the class of RSP–games was studied for purely theoretical reasons. I hope that it has become clear that these games are ideally suited for exemplifying the various incongruities between the game theoretical and the dynamical approach towards frequency dependent selection. However, RSP–games form a generic class of games and more than 1.5% of all 3x3 normal form games belong to this class.[2] It should, therefore, not be too surprising to find RSP–like game structures in biological populations. It is quite conceivable that, for example, strain A of a bacterial species outcompetes strain B in direct competition, strain B outcompetes strain C and strain C outcompetes strain A. A situation like this has, in fact, been observed during selection experiments in a chemostat.

A 'chemostat' is basically a device that enables a microbial culture to be maintained in permanent exponential growth in a constant and homogeneous environment (see, e.g., Dykhuizen & Hartl 1983). The growth medium is a chemically defined salt solution supplemented with a source of carbon and energy. Concentrations of the components of the fresh medium entering the growth chamber are such that only one (the limiting nutrient) is exhausted by the culture. Competition for the limiting resource leads to selection between different strains of microorganisms. Since it is fairly easy to follow a chemostat for several hundred generations, this device has proven valuable for detecting very slight selective differences between pairs of genotypes. In fact, chemostat experiments are sufficiently reproducible that differences in growth rates as small as 0.5% per generation are readily detected in replicate experiments (Dykhuizen & Dean 1990).

Quite often, long–term selection experiments in a chemostat yield rather unexpected results (see, e.g. Dykhuizen 1990). Charlotte Paquin and Julian Adams (1983), for example, analysed the competition between different asexual strains of the yeast *Saccharomyces cerevisiae* in a glucose–limited chemostat. All strains originated from an ancestral strain and they only differed from another by having accumulated a different number of mutations in the course of the experiment. Let us concentrate on their first experiment with a haploid yeast population and let H_i denote the strain isolated in generation i. (Virtually the same results were obtained for a diploid yeast population.) Paquin and Adams carefully analyzed the pairwise competition between strains H_{30}, H_{133} and H_{203} which, compared to the ancestral strain H_0, presumably had accumulated 0, 2 and 3 adaptive mutations respectively. As expected, each strain had a 'selective advantage' when compared to the previous one: H_{133} outcompeted H_{30} in pairwise competition, and H_{203} in turn outcompeted H_{133}. Rather unexpectedly, however, selection advantage was not transitive since the older strain H_{30} outcompeted the derived strain H_{203} in direct competition. It is tempting to speculate that the yeast populations in Paquin and Adams' experiments evolve under frequency dependent selection with the same intransitivities in pairwise competition that are so characteristic for the class of RSP–games.

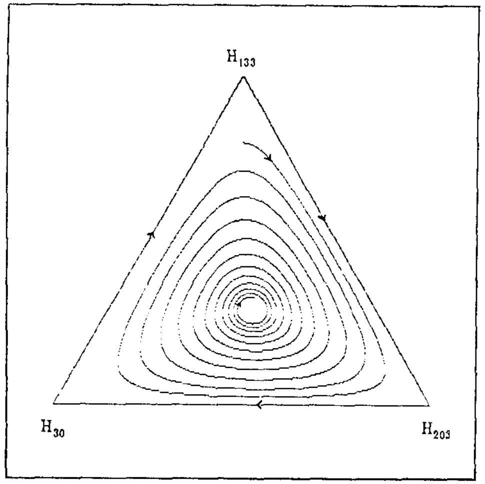


Figure 10: Orbit of the continuous replicator dynamics induced by the RSP–game (8.1).

The experiments described above were performed with large (about $5 \cdot 10^9$ individuals per population) asexual populations with a very short generation time (about six generations per day). These are precisely the circumstances to which the continuous replicator dynamics does apply. Paquin and Adams (1983, Table 1) determined the relative fitness of the three strains H_{30}, H_{133} and H_{203} in pairwise competition. Their results may be summarized by the payoff matrix

$$A = \begin{bmatrix} 1.00 & 1.18 & 0.88 \\ 0.85 & 1.00 & 1.16 \\ 1.13 & 0.86 & 1.00 \end{bmatrix}, \tag{8.1}$$

where the pure strategies 1, 2 and 3 correspond to the strains H_{30}, H_{203} and H_{133} respectively. Let us assume that the RSP–matrix A of relative fitness values is pl–equivalent to the matrix of absolute fitness values and that selection is indeed linearly frequency dependent (i.e., that the fitness function is given by (2.3)). Then a stable polymorphism of all three strains is to be expected (see Figure 10). Unfortunately, Paquin and Adams never put all three strains in competition. Thus, it remains unclear whether the theoretical prediction will be experimentally confirmed or not.

Like many other authors in the chemostat literature, Paquin and Adams notice a discrepancy between their results and the 'classical' predictions of (frequency independent) selection theory. However, they do not ascribe their results to frequency dependent selection but to other evolutionary forces like epistatic interactions between different muations. In my view, the possibility of frequency dependent selection is grossly underestimated in the chemostat literature. In a situation where the 'external' (abiotic) environment is held as constant as possible, the selective forces should to a large extent be governed by intraspecific interactions which, almost invariably, lead to frequency dependent selection. Many puzzling results in the chemostat literature (e.g. Helling et al. 1987, Bennett et al. 1990) can be explained much more naturally if frequency dependent selection is taken into consideration.

Notes:

1. It can be shown that a Nash equilibrium in the barycenter $\mathbf{m}$ of the strategy simplex is an ESS if and only if the trajectories of the continuous replicator equation starting close to $\mathbf{m}$ are attracted *monotonically* by $\mathbf{m}$ (with respect to the usual Eucledian metric). One might conjecture that $\mathbf{m}$ can only be a non–ESS attractor, if some form of cycling takes place, i.e. if the Jacobian of the continuous replicator dynamics at $\mathbf{m}$ is not diagonalizable in the real domain. The following payoff matrix provides a counter–example to that conjecture:

$$A = \begin{bmatrix} 0 & 19 & 1 \\ 19 & 0 & 1 \\ 1 & 19 & 0 \end{bmatrix}.$$

In that example, $\mathbf{m}$ is an attractor which is not an ESS. The eigenvalues of the Jacobian at $\mathbf{m}$ are real and distinct ($-1/60$ and $-19/60$). Accordingly, the Jacobian is diagonalizable and there is no cycling around $\mathbf{m}$.

2. RSP–games form a generic class of symmetric normal form games, i.e. a class of games of full dimension. If the elements of a 3x3 payoff matrix A are drawn at random from a uniform distribution, an RSP–game will result with probability $1/64$.

3. Adding $\eta := -\epsilon/2$ to the ϵ–perturbed Rock–Scissors–Paper game

$$A_\epsilon = \begin{bmatrix} 0 & 1+\epsilon & -1 \\ -1 & 0 & 1+\epsilon \\ 1+\epsilon & -1 & 0 \end{bmatrix}, \quad \epsilon > -1, \tag{1.4a}$$

yields an RSP–game of the form

$$B_\eta = \begin{bmatrix} \eta & 1-\eta & -1+\eta \\ -1+\eta & \eta & 1-\eta \\ 1-\eta & -1+\eta & \eta \end{bmatrix}, \quad \eta < 1/2. \tag{1.4b}$$

Dividing B_η by $1-\eta$ and setting

$$\delta := \frac{\eta}{1-\eta} = \frac{\epsilon}{2+\epsilon},$$

one arrives at the RSP–game

$$C_\delta = \begin{bmatrix} \delta & 1 & -1 \\ -1 & \delta & 1 \\ 1 & -1 & \delta \end{bmatrix}, \quad -1 < \delta \leq 1, \tag{1.4c}$$

which is payoff equivalent to A_ϵ and B_η.

4. Theorem 3.4. shows that, in evolutionary 3x3 normal form games which are *not* RSP–games, a discrepancy between evolutionary stability and continuous dynamic stability is always associated with the the existence of nontrivial border fixed points of the replicator dynamics. Non–RSP examples are in that sense more complicated than the games analyzed in this paper. However, they may show some additional features that are missing in the context of RSP–games. Zeeman (1980), for instance, presents a nice example which is based on the payoff matrix

$$A = \begin{bmatrix} 0 & 6 & -4 \\ -3 & 0 & 5 \\ -1 & 3 & 0 \end{bmatrix}.$$

Here, the barycenter **m** is an attractor that coexists with the unique ESS which is given by the pure strategy *1*. Although **m** is not an ESS, its domain of attraction is larger than that of the ESS. The fact that **m** is not a global attractor points out another *qualitative* difference between evolutionary stability and dynamic stability: A completely mixed ESS is always a global attractor for the continuous replicator dynamics (see Corollary 5.2) whereas completely mixed non–ESS attractors may coexist with boundary attractors.

5. An alternative proof may be based on the theorem of Poincaré–Hopf (see e.g. Hofbauer & Sigmund 1988, Chapter 19). This theorem can be applied to a slight modification of the flow which is induced by an RSP–game on the border of the strategy simplex (see (1.2)). As a result one gets that the sum of the Poincaré–indices of the interior fixed points of the replicator dynamics is equal to one, the Euler characteristic of the strategy simplex. This implies the existence of at least one interior fixed point which is automatically a Nash equilibrium strategy. In view of the uniqueness result in Theorem 3.3, there exists a unique interior fixed point, and the Poincaré–index of this fixed point is equal to one. If this fixed point is regular, we get some additional information: the fixed point is necessarily either a sink, a source, or a center.

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